ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde

Volume 59, 1994 ISSN 0044-3468

Mit 140 Abbildungen

Verlag Paul Parey Hamburg und Berlin

Wissenschaftliche Originalarbeiten

Wissenschaftliche Kurzmitteilungen

Mitteilungen der Gesellschaft

Buchbesprechungen

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

 Verlag: Paul Parey GmbH & Co. KG, Hamburg. Anschrift: Spitalerstraße 12, D-20095 Hamburg, Bundesrepublik Deutschland. Printed in Germany by Westholsteinische Verlagsdruckerei Boyens & Co., Heide/Holstein

ISSN 0044-3468 59 (1–6) 1–384 (1994)

Vol. 59 (1), 1–64, Februar 1994 ISSN 0044-3468 C 21274 F

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Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologiezentrum der Christian-Albrechts-Universität, Am Botanischen Garten 9, D-24118 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

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Z. Säugetierkunde 59 (1994) 1–8

ISSN 0044-3468

Seasonal variation in diet and trophic niche of the Red fox in an Alpine habitat

By M. LUCHERINI and GIULIA CREMA

Department of Evolutionary Biology, Ethology and Behavioural Ecology Group, University of Siena, Siena, Italy

Receipt of Ms. 30. 10. 1992
Acceptance of Ms. 23. 4. 1993

Abstract

The diet and trophic niche breadth of the fox (*Vulpes vulpes*) were studied in a high-elevation Alpine ecosystem to determine their monthly variations. The analysis of 270 faeces showed that the fox used all the potential resources present in its habitat: of total diet, small mammals were the most frequent food category, but Orthoptera and marmots were also very important. Correlations between diet and weather variables suggested a seasonal shift in diet. From June to November foxes preyed mainly on insects and marmots, whereas ungulates, Lagomorpha, garbage and earthworms were eaten more often from December to May. These changes appeared related both to seasonal differences in food availability and to the presence of alternative preferred foods. Trophic niche was wide during the entire year, with a moderate increase in winter–spring when the absence of some main prey types forced the fox to exploit a larger range of items.

Introduction

The adaptable behaviour of the red fox has enabled it to colonize a variety of habitats, including those typically montane (MACDONALD 1987). Although the fox is probably the most common carnivore in the Alps, only two recent studies (CANTINI 1991; STORCH and KLEINE 1991) have dealt with the diet of the fox in the Alpine region, and both were carried out at elevations between 300 and 1700 m. The diet of the fox in the highest part of its altitudinal distribution in Europe has been locally investigated only by LEINATI et al. (1960).

Montane ecosystems are strongly seasonal in terms of climate and productivity. Given the opportunistic feeding habits of the fox (e. g. ENGLUND 1965; GOSZCZYNSKI 1986; CALISTI et al. 1990), it can be expected that its diet in the Alps would largely reflect the seasonal changes in food availability.

Our study area, in the Italian Western Alps, is frequented by at least 370 Alpine chamois (*Rupicapra rupicapra*) (minimum density: 10 individuals/km^2), about 20 Alpine ibex (*Capra ibex*), at least 25 roe deer (*Capreolus capreolus*) and 5–15 red deer (*Cervus elaphus*). Furthermore, although no estimates are available, the study area supports wild boars (*Sus scrofa*) and dense populations of Alpine marmot (*Marmota marmota*) and insects (mainly Orthoptera). The results of the research conducted in the Alps by LEINATI et al. (1960) showed that ungulate carrion, especially in late winter, and marmots, in summer, are well represented in the fox diet in the Alps, but did not include Orthoptera among the most important food items. Nevertheless, since strong predation on Orthoptera has been reported in other habitats (CALISTI et al. 1990 for a review), we expected that the local abundance of marmots and Orthoptera would largely influence the diet of the fox in the months when they are available. The densities of small mammals in the study area were not known, but they can also be a main component of the fox diet, as found in northern highly seasonal habitats (LINDSTRÖM 1989).

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The aim of this paper is to present a picture of the seasonal variation of the fox trophic niche in a typical Alpine ecosystem. We were particularly interested in determining the extent of fox predation on marmot and Orthoptera and in documenting the use of ungulate carcasses.

Study area

The study area in the Western Italian Alps, about 80 km west of Torino, comprises the Val Troncea Natural Park (3280 ha) and the small part of the homonymous valley at lower altitude outside the park boundaries. Elevation ranges from 1560 m to 3280 m a. s. l. Topography, vegetation and climate of the valley are typically Alpine. Precipitation peaks in spring and autumn, while winter is characterised by 4–6 months of permanent snow cover and low temperatures. Mean annual temperature is about 8 °C (Fig. 1). Larch (*Larix decidua*) forests and pastures cover the slopes to about 1900–2100 m, while Alpine meadows are prevalent at higher altitudes. At the end of the valley lies a small tourist village, inhabited mainly during summer and Christmas holidays. Many tourists visit the park from May to August.

Material and methods

From May 1990 to June 1991, 3–4 monthly collections of faecal samples were made at elevations between 1560 and 2850 m. In a total of 46 excursions on foot or skis 270 faeces were collected (sample size: May: 4; Jun: 25; Jul: 16; Aug: 18; Sep: 44; Oct: 23; Nov: 31; Dec: 7; Jan–Feb: 16; Mar: 26; Apr: 15; May 1991: 22; Jun 1991: 23). On the two trails followed each month, all scats were collected; outside these trails, only obviously fresh samples were collected. Scats were stored in polythene bags and frozen at −20 °C, to be thawed later and analysed as described in Kruuk and Parish (1981), Ciampalini and Lovari (1985) and Calisti et al. (1990). To allow comparisons with other studies, results are reported as percentage of occurrence (number of occurrence of each food/total number of occurrences × 100) (Cavallini and Lovari 1991), percent frequency of occurrence (number of occurrence of each food/number of faeces × 100), and percentage of volume (estimated volume of each food/total estimated volume × 100) (Kruuk and Parish 1981). In February we only found two scats, therefore we pooled data for January and February. In winter, frequent snowfalls often prevented faecal collections, both by limiting the movements of the foxes and rapidly covering tracks and scats (Patalano and Lovari 1993). As a result, more faecal samples were found during summer–autumn. In the evaluation of the total yearly diet, scats collected in May 1990 and June 1991 were excluded so that each month would be represented only once. The total percentages of occurrence and volume were computed as means of monthly values.

A standardized index of trophic niche breadth (B_{sta}) (Colwell and Futuyma 1971) was calculated from both percentages of occurrence and percentages of volume. The index has the formula $B_{sta} = B-1/B_{max}-1$, where B is the Levins' index of niche breadth (Levins 1968) and B_{max} is the total number of food categories recognized. B_{sta} values can range between 0 (minimum niche breadth) and 1 (maximum niche breadth).

The availability of Orthoptera was estimated by direct counts of the number of individuals seen along two fixed transects (100 m each) (Cavallini and Lovari 1991). One transect was located in pastures at 1900 m, the other in Alpine meadows at 2200 m.

To identify seasonal variations in consumption of the main food categories, Spearman rank correlations (Siegel 1956) were performed between percentages of occurrence and volume and climatic variables (Calisti et al. 1990; Cavallini and Lovari 1991). Differences between summer–autumn and winter–spring diets were tested with a G-test of independence (Sokal and Rohlf 1981) on the occurrences (expressed as frequencies of scats where the category was found over the total number of scats) and with Mann-Whitney U-test (Sokal and Rohlf 1981) on volumes. Values of p less than 0.05 were considered significant.

Results

Diet

In the total diet, the most frequent and abundant prey remains were of small mammals (mainly Arvicolidae, followed by Muridae) (Tab. 1), with little seasonal variation (Fig. 2). Orthoptera, which were only available from June to November (Fig. 1) and consumed mainly from August to November (Fig. 2), were nevertheless the second most important

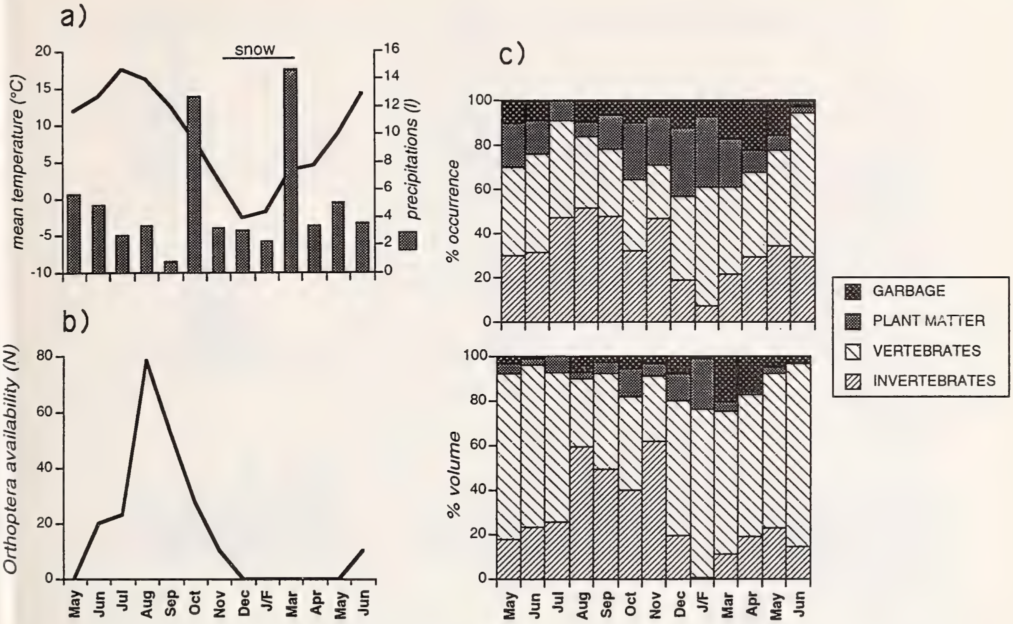

Fig. 1. Monthly changes of: a) Mean temperature and precipitation in the study area; b) Orthoptera availability in the study area; c) Percent occurrence and volume of the main groups of food categories in the diet of the red fox in Val Troncea

category in the annual diet (Tab. 1). Alpine marmots (often young individuals) and wild ungulates (mostly carcasses of Alpine chamois and roe deer, but also some young of roe deer and wild boar) were the only other items accounting for more than 10 % of total volume, but their occurrences were remarkably lower (Tab. 1). The presence of marmot in the diet showed a peak in June–July, whereas that of ungulates was higher in January–February than in the rest of the year (Fig. 2). Coleoptera remains were found in all months except December (Fig. 2). They were eaten very often but usually in small amounts (Tab. 1; Fig. 2). A similar discrepancy between occurrences and volumes was shown by Lepidoptera larvae and earthworms (Tab. 1). As a whole, fruits were found in almost 15 % of the scats and composed 4.5 % of the annual volume, but the main kind of fruits eaten by the fox (*Rosa* sp. fruits) did not reach 3 % of the volume (Tab. 1). More important was the role of garbage, which was present in 21 % of all the scats with a total volume of 6.6 % (Tab. 1). Birds (mainly Passeriformes) and Lagomorpha (mainly mountain hare, *Lepus timidus*) were seldomly consumed by foxes in the Troncea valley (Tab. 1).

Overall, vertebrates composed the bulk of the diet (38.2 % occurrence and 56.2 % volume; see also Fig. 1). The seasonal pattern of use of this food source was rather constant, with a moderate decrease during summer (Fig. 1). Invertebrates (33.3 % occurrence and 30 % volume) showed the opposite trend, decreasing markedly during winter (Fig. 1). Plant matter and garbage were taken mainly in winter and early spring, respectively (Fig. 1).

Correlations

In most cases, correlations between diet and main climatic variables confirmed the seasonality described above for some food categories (Tab. 2). Coleoptera consumption was inversely correlated to snow cover (percentage of days with snow-covered ground) and directly to mean temperature. The presence of marmot in diet showed the same kind of

Table 1. **Annual diet composition of the red fox in the Val Troncea Natural Park**
(n = 243 faecal samples)

Food items	% freq. occ.	% occ.	% vol.
Coleoptera	29.6	10.5	5.3
Orthoptera	42	12.9	16.7
Dermaptera	4.9	1.6	0.4
Coleoptera larvae	1.7	0.7	0.7
Lepidoptera larvae	15.6	4.8	2.6
Diptera larvae	3.7	1.1	0.7
Earthworms	18.5	7.3	3.7
Other invertebrates	0.8	0.2	0.1
Small mammals	44.4	17.1	21.6
Marmots	18.1	6.3	12.7
Lagomorpha	4.5	1.8	3.2
Ungulates	12.4	5.7	11.6
Other mammals	3.7	1.7	2.5
Birds	9.9	3.9	3.7
Reptiles	1.7	0.8	0.9
Amelanchier ovalis fruits	2.1	0.8	0.2
Rubus sp. fruits	2.1	0.8	1.0
Rosa sp. fruits	6.2	3.1	2.4
Other fruits	4.1	1.6	0.9
Other plant matter	24.3	9.1	2.8
Garbage	21.0	8.3	6.6
B_{sta}		0.50	0.37

B_{sta}: standardized trophic niche breadth index (see text).

Table 2. **Correlations, on a monthly basis, of food categories in diet with mean temperature (°C), precipitations (ml) and snow cover (% days with snow-covered ground)**
(n = 13 months)

Food items		Mean temp.		Precipitations		Snow cover	
		r_s	p	r_s	p	r_s	p
Coleoptera	freq. occ.	0.835	**	0.271	0.35	−0.621	*
	occ.	0.896	**	0.202	0.48	−0.615	*
	vol.	0.732	0.17	0.396	AS	−0.474	0.17
Marmots	freq. occ.	0.865	**	0.514	AS	−0.538	AS
	occ.	0.865	**	0.544	AS	−0.514	AS
	vol.	0.849	**	0.56	*	−0.514	AS
Ungulates	freq. occ.	−0.46	0.11	−0.235	0.42	0.452	0.12
	occ.	−0.42	0.15	−0.262	0.36	0.435	0.13
	vol.	−0.427	0.14	−0.161	0.58	0.386	0.18
Fruits	freq. occ.	−0.202	0.48	−0.312	0.28	0.556	*
	occ.	−0.521	AS	−0.284	0.32	0.689	*
	vol.	−0.606	*	−0.327	0.26	0.713	*

AS = almost significant ($0.10 > p > 0.05$); * = $p < 0.05$; ** = $p < 0.01$.

correlations as Coleoptera and a tendency to increase with precipitation. Fruits were eaten more frequently during cold and snowy months than during the rest of the year. This seemed also to be the case for ungulates, but significance was not reached. No trend was shown by Orthoptera, small mammals and garbage. Use of Orthoptera increased together with their estimated availability (occurrence: $r_s = 0.570$, $p < 0.05$; frequency of occurrence:

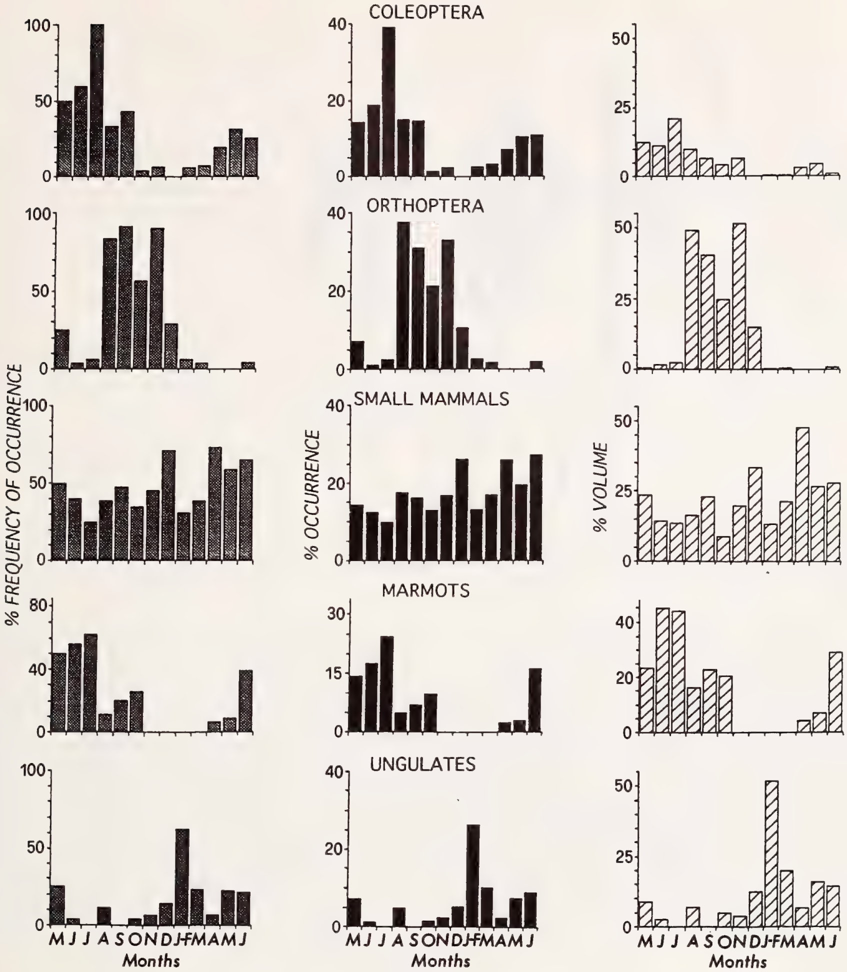

Fig. 2. Monthly variation of the main food categories in the red fox diet

$r_s = 0.587$, $p = 0.05$; volume: $r_s = 0.747$, $p = 0.01$; $n = 13$ months). No seasonal pattern was found for the variation of trophic niche breadth (B_{sta} values; in occurrences, May: 0.358; Jun: 0.374; Jul: 0.167; Aug: 0.19; Sep: 0.252; Oct: 0.433; Nov: 0.234; Dec: 0.267; Jan–Feb: 0.315; Mar: 0.369; Apr: 0.306; May 1991: 0.361; Jun 1991: 0.129; in volumes, May: 0.141; Jun: 0.153; Jul: 0.14; Aug: 0.122; Sep: 0.153; Oct: 0.323; Nov: 0.11; Dec: 0.228; Jan–Feb: 0.109; Mar: 0.256; Apr: 0.133; May 1991: 0.298: Jun 1991: 0.196) and no significant correlation between it and the monthly percentages of the main food categories or the number of scats collected each month.

Seasonality

Two main periods were distinguished in the diet of the fox in the study area on the basis of its monthly variation and the correlations shown by the main food categories (Fig. 3). From June to November foxes ate more insects (Orthoptera: occurrence $G = 91$, $p < 0.001$; volume $Z = -2.37$, $p < 0.05$; Coleoptera: occurrence $G = 19.8$, $p < 0.001$; volume Z

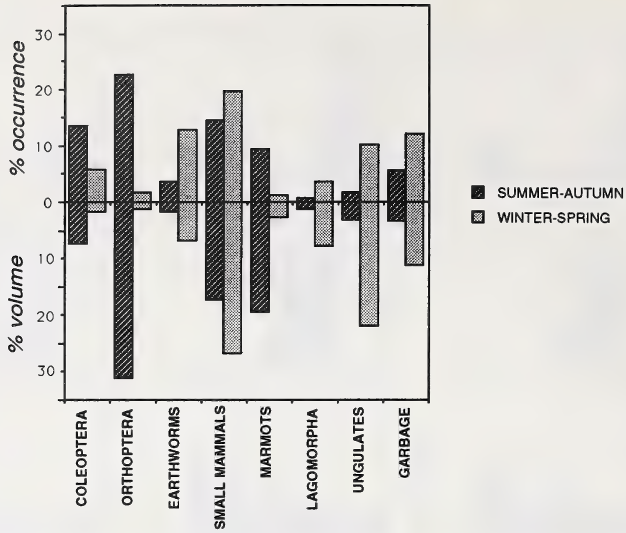

Fig. 3. Percent occurrence and volume of the main red fox food categories in summer–autumn and winter–spring diets

= −2.01, $p < 0.05$) and marmots (occurrence G = 23.4, $p < 0.001$; volume Z = −1.73, $p < 0.08$) than from December to May. Conversely, ungulates (occurrence G = 24.4, $p < 0.001$; volume Z = −2.56, $p < 0.05$), Lagomorpha (occurrence G = 6.6, $p = 0.001$; volume Z = −1.1, $p = 0.27$) garbage (occurrence G = 26.9, $p = 0.001$; volume Z = −1.46, $p = 0.14$) and earthworms (occurrence G = 19.4, $p < 0.001$; volume Z = −1.55, $p = 0.12$) appeared to be more frequent in winter–spring than in summer–autumn. Small mammals did not show significant seasonal differences (occurrence G = 2.4, $p = 0.06$; volume Z = −1.64, $p = 0.10$).

The winter–spring diet was dominated by mammals (62.8 % volume; see also Fig. 3). Nevertheless, the trophic niche appeared to be larger in this period (occurrence B_{sta} = 0.489; volume B_{sta} = 0.316) than in summer–autumn (occurrence B_{sta} = 0.372; volume B_{sta} = 0.234), although the difference did not reach significance (T-test: t = 5.7, $n = 2$, $p = 0.055$).

Discussion

Our data show that the fox can use all the potential sources of food present in its habitat. Small mammals, Orthoptera, marmots and ungulates supplied the fox with protein-rich food items. In particular, our results suggest that, as could be expected on the basis of their qualitative analysis (Cavani 1991), Orthoptera can be an important food resource not only in warm Mediterranean habitats (Calisti et al. 1990), but also in elevated Alpine regions (see also Patalano and Lovari 1993, for the Italian Apennines). In a similar area, Leinati et al. (1960) found a greater presence of vegetables and ungulate carrions and a lower existence of invertebrates in the fox diet. These differences are likely to be related to the local variation of food availability and also to the inclusion of lower-altitude ranges in the study area of Leinati et al.

In our study area, the diet of the fox reflected the alternation of two main seasons typical of the montane ecosystems (Patalano and Lovari 1993). As shown for Orthoptera (see the correlations between availability and consumption), the temporal variation in feeding habits was likely to be mainly determined by the availability of different food

resources (DONCASTER et al. 1990; CAVALLINI and LOVARI 1991). For example, insects and marmots are unavailable in winter, and were present almost exclusively in the summer–autumn diet. As could be expected, the winter peak in mountain ungulate mortality (e. g. GEIST 1971; FESTA-BIANCHET 1989) was reflected by an increase of this item in winter diet. The higher percentage of earthworms in the cold season may appear surprising. Actually, the use of this food was concentrated in the months between March and May, the only months when soil temperature and humidity were probably high enough to permit frequent earthworm activity on the ground (KRUUK and PARISH 1985; LAMBERT 1990). Therefore, the variation in the consumption of this invertebrate may also be explained by that of its availability. On the other hand, the increased use of certain food categories in winter–spring would confirm the influence of the availability of alternative food resources on the feeding behaviour of an opportunistic carnivore, as suggested by WECKWERTH and HAWLEY (1962). In our study area, garbage is mostly available during the summer months, when tourists are numerous. Nevertheless, rubbish remains were found in the scats mainly in winter. During this season important food items (i. e. insects and marmots) were absent and the fox exploited other resources, less preferred (i. e. garbage) or difficult to obtain (i. e. Lagomorpha).

The seasonality of the diet was not clearly reflected by the trophic niche size, as found in other areas (CALISTI et al. 1990). If the number of scats collected each month is not large enough to be representative of the diet, the monthly value of niche breadth index might be influenced by sample size. No evidence of such a relation was found (correlations between B_{sta} values and monthly number of scats collected were far from significant) (IRIARTE et al. 1990). PRIGIONI (1991) reviewed studies of fox diet in Italy and calculated for them an index of trophic niche breadth on a reduced number of main categories. The application of the same method shows that, in our study area, the fox has a very wide trophic niche. These findings could suggest that the lack of correlation between trophic niche breadth and climatic variables in our study might have been more correctly related to its large breadth (cf. CALISTI et al. 1990) than to uncorrect sampling. In the Troncea Valley, the fox had a varied diet in each period of the year, with a moderate widening of the trophic niche during winter–spring. This variation was likely due to the increased presence in the diet of "secondary" items (e. g. garbage, fruits, Lagomorpha) in cold months, when some main food categories are absent and the fox is forced to exploit a larger array of items to meet its nutritional requirements.

Acknowledgements

We wish to thank M. FESTA-BIANCHET, S. LOVARI and two anonymous referees, whose suggestions greatly improved our first draft. We are grateful to the staff of the Val Troncea Natural Park, which helped us in many ways. The abstract was kindly translated by U. BREITENMOSER. The research was partially supported by the Val Troncea Natural Park, Italy, and by a grant to S. LOVARI from Italian Ministry of Education.

Zusammenfassung

Saisonale Variabilität von Nahrung und trophischer Nische beim Fuchs in alpinem Habitat

Mit dem Ziel, die monatliche Variabilität zu bestimmen, untersuchten wir die Nahrungswahl und die trophische Nische des Fuchses (*Vulpes vulpes*) in höheren alpinen Stufen. Die Analyse von 270 Exkrementen zeigte, daß sämtliche in diesem Habitat vorhandenen Nahrungsquellen genutzt wurden. In der gesamten Nahrung waren Kleinsäuger die am häufigsten gefundene Nahrungskategorie, gefolgt von Orthopteren und Murmeltieren. Korrelationen zwischen Nahrung und Klimavariablen wiesen auf einen saisonbedingten Wechsel in der Nahrungswahl hin. Von Juni bis November erbeuteten die Füchse hauptsächlich Insekten und Murmeltiere, während von Dezember bis Mai häufiger Ungulaten, Lagomorphen, Abfälle und Regenwürmer gefressen wurden. Dieser Wechsel scheint sowohl mit saisonalen Unterschieden in der Verfügbarkeit von Futter als auch mit dem Angebot an bevorzugter Alternativnahrung zusammenzuhängen. Die trophische Nische war während des ganzen Jahres breit und zeigte eine leichte Ausweitung im Winter und Frühjahr, wenn das Fehlen einiger Hauptbeuten die Füchse veranlaßte, ein breiteres Nahrungsangebot zu nutzen.

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Authors' addresses: Mauro Lucherini, Dipartimento di Biologia Evolutiva, Università di Siena, V. Mattioli 4, I-53100, Siena, Italy, and Giulia Crema, Estación Biológica de Doñana, C. S. I. C., Apartado 1056, E-41080 Sevilla, Spain

Z. Säugetierkunde 59 (1994) 9–13
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ISSN 0044-3468

Activity of foxes, *Vulpes vulpes*, in the Swiss Jura mountains

By J.-M. Weber, J.-S. Meia, and S. Aubry

Institut de Zoologie, Université de Neuchâtel, Neuchâtel, Switzerland

Receipt of Ms. 26. 1. 1993
Acceptance of Ms. 21. 9. 1993

Abstract

Studied the activity pattern of seven radio collared foxes in a mountainous habitat in Switzerland. Foxes were mainly nocturnal and their nocturnal activity pattern was acyclic. Activity periods varied according to seasons, being shortest during summer. On the other hand effective activity did not vary significantly throughout the year. Fox active period was generally interrupted by several inactive phases, most of which were short (< 15 min.).

Introduction

Red fox activity has been studied in different lowland habitats (Ables 1969; Artois 1985; Woollard and Harris 1990 amongst others), but little is known of red fox activity in mountainous habitats. In their study of fox habitat use in the Swiss Alps, Capt and Stalder (1988) emphasized the nocturnal pattern of fox activity. Most authors usually described fox activity pattern and its variations in general terms (e.g., Artois 1989). There are few quantitative data about activity level and time budget. Recently, Woollard and Harris (1990) recorded the duration of inactive and active bouts occurring during the active period of urban foxes.

Therefore, the objective of this study is to describe the activity pattern and to quantify the activity level of foxes in a mountainous habitat.

Material and methods

This study was carried out in a rural area of the Swiss Jura mountains (47°09′ N, 6°56′ E; altitude: 995 to 1288 m). This area is mainly composed of pastures and wooded pastures, as described by Weber and Aubry (1993).

Seven vixens (F2, F3, F8, F10, F11, F12, and F19) were tracked between September 1989 and May 1992. The foxes were snared, and then tranquilized with an injection of ketamin hydrochloride. Each fox was tagged with 1 or 2 colored eartags (Dalton Supplies, Ltd., Henley-on-Thames, UK). Adult-sized individuals were fitted with activity monitoring transmitters (Wildlife Materials, Inc., Carbondale, Ill., USA).

Radio tracking data were collected in two different ways. Radio tagged animals were located daily (1 fix/fox/day) to determine their diurnal resting sites. The collared animals were also tracked for one 24-h period (12.00 to 12.00; 1 fix/15 min.) one day per week during the first month following their capture. They were then tracked for 24 hours (1 fix/15 min.) once every two weeks. Radio tracking was made either by car or on foot using portable telemetry equipment.

Variations in radio signal pulse rate indicated whether foxes were moving (active) or not (inactive); hence fixes were recorded as either active or inactive. Two periods were distinguished within a day: the daytime/daylight (dawn to dusk) and the nighttime (dusk to dawn). The total active fixes (diurnal and nocturnal) constituted fox effective activity (EA). The activity period (AP) was determined by nocturnal active and inactive fixes as well as diurnal activity fixes. A prolonged inactive phase (> 1 min.) during the nocturnal activity period was considered as "rest during the active period" (RAP).

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Results and discussion

Activity period and seasonal variations

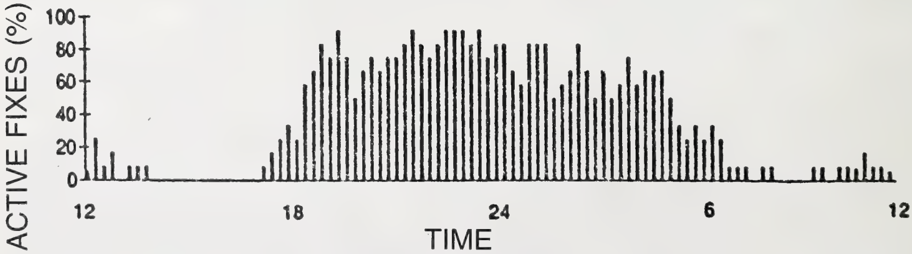
The activity period (AP) of all vixens was mainly nocturnal, but the individuals were also active to different degrees in daylight (Tab. 1). Two foxes (F2 and F3) were seldom or never active in the daytime (1.7 % (9/546) and 0 % (0/107) of diurnal active fixes respectively). Other vixens were significantly more diurnal (χ^2 test, $p < 0.05$). For F8, F10 and F19, the total proportion of diurnal active fixes did not exceed 9 %, whereas it represented 15.4 % and 11.7 % for F11 and F12, respectively. There was no significant trend in seasonal variations, but some individuals were more diurnal in one season than in another: F11 was more active during daytime in winter than in spring and summer (χ^2 = 108.89, d.f. = 2, $p < 0.001$).

Table 1. **Seasonal frequency (%) of diurnal active fixes recorded in foxes**
n: number of diurnal active fixes

	Spring		Summer		Autumn		Winter		Total	
	%	n	%	n	%	n	%	n	%	n
F2	–	–	–	–	0.4	288	3.1	258	1.7	546
F3	–	–	–	–	0.0	107	–	–	0.0	107
F8	4.8	209	–	–	–	–	5.9	169	5.3	378
F10	–	–	–	–	3.8	291	10.8	147	6.2	438
F11	13.5	244	11.8	340	–	–	38.4	73	15.4	657
F12	16.8	202	10.6	398	6.2	225	19.1	84	11.7	909
F19	7.1	227	14.1	191	9.8	225	4.1	267	8.4	910

Ables (1969) noticed that such variations could be influenced by climatological factors, for instance shorter diurnal activity in summer due to higher temperature and insolation. Eguchi and Nakazono (1980) emphasized human disturbance as a possible cause of fox diurnal activity, at least for individuals which were resting above ground during daytime.

Although we did not quantify the climatological factors, it seems that their influence was negligible, since there was no seasonal trend in diurnal activity. However, extreme weather conditions during the night could contribute to an increase of diurnal activity. This was observed for F11 during winter, when some nights were cold (ca. −25 °C.) On the other hand, we consider the human factor as very important. The high hunting pressure occurring in the region probably induced a nocturnal pattern of activity. In areas where cover was scarce, some foxes (F2 and F3) spent the day in dens and were strictly nocturnal most probably for safety reasons. For other foxes, diurnal activity was usually limited to movements between resting sites (Meia and Weber 1993). Foraging activity was uncommon in daylight, and even F8 did not show any increase of diurnal activity when rearing cubs during spring as described for another breeding vixen (Phillips and Catling 1991).



Example of fox activity pattern. F10: autumn and winter

The nocturnal activity pattern of the seven vixens was acyclic (Fig. 1). Most authors found a cyclicity in fox nocturnal activity pattern, being either bimodal (Ables 1969; Artois 1985) or trimodal (Eguchi and Nakazono 1980). According to Ables (1969), fox activity peaks were synchronized with those of the prey. In our study area, the main prey of foxes was the water vole, *Arvicola terrestris scherman* (Weber and Aubry 1993). Little is known about its activity pattern, but in Britain, no variation in activity was found between day and night (Boyce 1991). Our field observations indicated similar behaviour of water voles. No difference in trappability was found between day and night. Predators such as farm cats, *Felis catus*, and some raptors, regularly preyed on them in the daytime. This suggests a great variability in the activity pattern of water voles and could explain fox acyclic activity pattern in our study area to some extent.

There were seasonal variations in activity level of foxes (Tab. 2). Their activity period was shortest during summer and generally longest during winter (Mann-Whitney U test, $p < 0.05$). Besides, there were few variations between individuals. F12's autumn APs were longer than those of other foxes (Mann-Whitney U test, $p < 0.05$), and a similar trend was also observed in spring and summer.

Since fox activity period was mostly nocturnal in our area, the seasonal character of its duration was likely related to nighttime length (Eguchi and Nakazono 1980; Capt and Stalder 1988). Some intrinsic factors could explain the differences in the AP length observed between F12 and

Table 2. **Seasonal duration (min.) of fox activity periods, rest during the activity period and effective activity**
X: mean SD: standard deviation

	F2		F3		F8		F10		F11		F12		F19	
	X	SD	X	SD	X	SD	X	SD	X	SD	X	SD	X	SD
Activity period														
spring	-	-	-	-	557.1	147.6	-	-	717.8	107.9	741.4	81.6	617.5	70.6
summer	-	-	-	-	-	-	-	-	542.5	66.0	652.5	94.3	570.0	71.0
autumn	711.4	66.4	690.0	25.9	-	-	695.2	59.9	-	-	799.3	61.1	690.0	42.4
winter	797.5	68.9	-	-	753.0	144.7	795.0	114.2	622.5	289.4	690.0	207.8	762.8	64.5
Effective activity														
spring	-	-	-	-	454.3	168.1	-	-	527.1	104.4	443.6	93.6	547.5	73.3
summer	-	-	-	-	-	-	-	-	412.5	61.3	482.5	86.1	480.0	127.6
autumn	627.1	52.0	530.0	95.3	-	-	571.5	94.3	-	-	497.1	65.6	540.0	107.7
winter	602.5	133.6	-	-	506.0	144.7	525.0	199.4	461.3	198.8	410.0	233.5	574.2	61.1
Rest during AP														
spring	-	-	-	-	102.8	53.0	-	-	190.7	48.7	297.8	79.6	70.0	31.0
summer	-	-	-	-	-	-	-	-	130.0	32.4	170.0	114.9	90.0	61.5
autumn	84.3	40.6	160.0	110.6	-	-	123.7	54.2	-	-	302.1	95.8	150.0	96.3
winter	195.0	70.9	-	-	247.0	126.8	270.0	110.2	161.2	159.4	280.0	97.6	188.6	60.5

the other vixens. She was shot a few days before her capture, survived but never fully recovered. Because of her weak body condition, she probably needed to distribute her foraging effort over a longer period than other foxes.

Occurrence of rest during the activity period

Rest during the activity period (RAP) was related to AP length ($r_s = 0.69$, $n = 18$, $p < 0.01$). Longer activity periods led to more time spent resting. Variations between individuals also occurred. Compared to other vixens, and whatever the season was, F12 rested much longer during the activity period (Mann-Whitney U test, $p < 0.05$) (Tab. 2).

No correlation was found between foxes' effective activity (EA) and the length of activity period. Individual EA did not vary significantly throughout the year (Mann-Whitney U test, $p > 0.05$) (Tab. 2), but in some cases (e.g. F19) a 90 minutes difference could occur between the shortest and the longest EA.

Fox active period was generally interrupted by several inactive bouts. The average number of such breaks per night did not differ from one vixen to another, except F12 who used to take more breaks during her active period than F2, F8, F11 and F19 respectively (Student t-test, $p < 0.05$) (Tab. 3). The distribution of these breaks throughout the activity period did not follow any individual routine as also was observed in urban foxes (Woollard and Harris 1990). Their variable duration was classified into five groups (Tab. 3). For every fox, most of the inactive bouts were short (< 15 minutes) (Wilcoxon's signed-ranks test, $p < 0.05$), and on average occurred from 1.0 per night (F19) to 2.3 per night (F12). Intermediate (16–30; 31–45 minutes) and long resting periods (46–60; > 60 minutes) were less frequent. Only F8 and F12 used to rest on average once a night for more than 60 consecutive minutes, which was not surprising considering the presence of cubs to look after for F8 and the weak condition of F12.

Table 3. **Mean number of inactive bouts (IB) per night (X) according to their duration**
N: Total number of inactive bouts per fox, n: number of nights

	F2 (n = 13)		F3 (n = 3)		F8 (n = 12)		F10 (n = 12)		F11 (n = 17)		F12 (n = 23)		F19 (n = 25)	
IB	N	X	N	X	N	X	N	X	N	X	N	X	N	X
< 15	21	1.6	6	2.0	16	1.3	20	1.7	29	1.7	53	2.3	26	1.0
16–30	6	0.5	3	1.0	7	0.6	11	0.9	14	0.8	23	1.0	18	0.7
31–45	12	0.9	2	0.7	4	0.3	7	0.6	5	0.3	19	0.8	9	0.4
46–60	3	0.2	1	0.3	2	0.2	4	0.3	13	0.8	7	0.3	7	0.3
> 60	6	0.5	1	0.3	11	0.9	8	0.7	6	0.4	24	1.0	13	0.5
Total	48	3.7	13	4.3	40	3.3	50	4.2	67	4.0	126	5.4	73	2.9

The average duration of inactive bouts was shorter (except for F12) in our area than in an urban environment. Woollard and Harris (1990) recorded inactive bouts in Bristol averaging between 45.2 and 55.9 minutes, whereas our estimates ranged from 22.1 to 28.8 minutes (F12: 44.8 minutes). The comparatively higher diversity of potential food in the urban habitat as well as the smaller size of their home range (Harris 1980) could lead urban foxes to meet their daily energetic requirements more easily than mountain foxes, and accordingly to increase the duration of their resting periods.

Acknowledgements

We would like to thank Dr. R. Hewson for useful comments on the manuscript and Mr. N. Ferrari for help with the field work. We acknowledge the support received from Prof. C. Mermod. The study was funded by the Swiss National Fund, grant 31-27766.89/2.

Zusammenfassung

Aktivität des Rotfuchses, Vulpes vulpes, im Schweizer Jura

Die Aktivität von 7 weiblichen, mit Sendern versehenen Rotfüchsen wurde im Gebiet des Schweizer Jura studiert. Die Rotfüchse waren vor allem nachtaktiv und im allgemeinen azyklisch. Die Aktivitätszeiten waren in den Jahreszeiten unterschiedlich lang, die kürzesten fielen in den Sommer. Die effektive Aktivität erfuhr dagegen im Laufe des Jahres keine merklichen Veränderungen. Die Aktivitätsphasen der Rotfüchse wurden stets durch mehrere Ruhephasen unterbrochen. Die meisten davon waren kurz (< 15 Min.).

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Authors' address: Dr. Jean-Marc Weber, Jean-Steve Meia and Stéphane Aubry, Institut de Zoologie, Université de Neuchâtel, Chantemerle 22, CH-2000 Neuchâtel 7, Switzerland

Z. Säugetierkunde 59 (1994) 14–20

ISSN 0044-3468

Cytogenetic analysis of autosomal polymorphism in *Graomys griseoflavus* (Rodentia, Cricetidae)

By A. Zambelli, Lidia Vidal-Rioja, and R. Wainberg

Instituto Multidisciplinario de Biología Celular, La Plata, Argentina and Cátedra de Biología General, Departamento de Ciencias Biológicas, Facultad de Ciencias Exactas, Universidad Nacional de La Plata, Argentina

Receipt of Ms. 1. 12. 1992
Acceptance of Ms. 8. 6. 1993

Abstract

South American phyllotine *Graomys griseoflavus* specimens were collected in eight localities of central Argentina and cytogenetically analysed. These populations comprised the following karyomorphs: 2n = 42, 41, 38, 37, 36, 35 and 34. These chromosome polymorphisms resulted from Robertsonian fusions (RFs). A pericentric inversion (PI) in two different autosomal pairs are described. The numerical karyotype variability is explained by successive RFs, starting from a karyotype with 2n = 42.

Introduction

Graomys griseoflavus (Waterhouse, 1837) is a South American phyllotine rodent showing a high degree of chromosomal polymorphisms. Previously, Wainberg and Fronza (1974a, b) reported preliminary data in one population of Argentina that then was misdetermined as *Phyllotis griseoflavus griseoflavus*. Later, according to a revision of the taxa (Pearson and Patton 1976) these specimens were recognized as *Graomys griseoflavus* (Reig pers. comm.). Wainberg and Fronza (1974a, b) described diploid numbers of 2n = 38, 37 and 36 for specimens collected in Chasicó (Buenos Aires province, Argentina) and suggested RFs as a possible mechanism for the karyotypic variability found.

Some reports sustain the idea that rodents are in active speciation processes (Greenbaum et al. 1978; Hsu and Arrighi 1968; Reig 1984). Supporting evidence are chromosomal polymorphisms observed in many species. In *Mus domesticus* for instance, there were defined more than 110 different Robertsonian fusions (RFs). The presence of several Robertsonian populations is regarded as an example of stasipatric speciation (Redi and Capanna 1988). Cricetid rodents that show high chromosomal variability have been considered models for studies on chromosomal rearrangements, speciation and evolution (Bianchi et al. 1971, 1979; Hood et al. 1984; Nachman and Myers 1989; Nachman 1992). In the genus *Eligmodontia* Zambelli et al. (1992) described the occurrence of RFs in a polymorphic system 2n = 34-33-32, where the 2n = 33 (heterokaryomorph) males showed a trivalent in diakinesis-metaphase I. So far, in all the models described the contributing acrocentric chromosomes have a random chance to fuse.

In the present study we describe the so far unknown 2n = 42, 41, 35 and 34 karyomorphs of *G. griseoflavus* and present G-banding analysis that confirms the occurrence of RFs and pericentric inversions (PIs). We suggest a hypothesis explaining the karyotypic variability by successive RFs that occurred non-randomly.

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Material and methods

We processed seventy-two animals collected at the following eight localities of central Argentina (Fig. 1): Chasicó (Buenos Aires province); La Carrera (Catamarca province); Divisadero Largo (Mendoza province); Salicas and General Belgrano (La Rioja province) and Deán Funes, Laguna Larga and Santiago Temple (Córdoba province). Table 1 shows the number of specimens caught in each locality, and the diploid numbers (2n) found.

Bone marrow metaphase spreads were obtained by a modification of the technique of ROTHFELDS and SIMINOVICH (1958). To enhance bone marrow cell proliferation all specimens were previously treated with a yeast suspension (LEE and ELDER 1980). Meiotic preparations from testes were done as indicated by EVANS et al. (1964). Chromosomal G-banding was obtained according to SEABRIGHT (1971). Homozygous and heterozygous terms were abbreviated Hm and Ht, respectively.

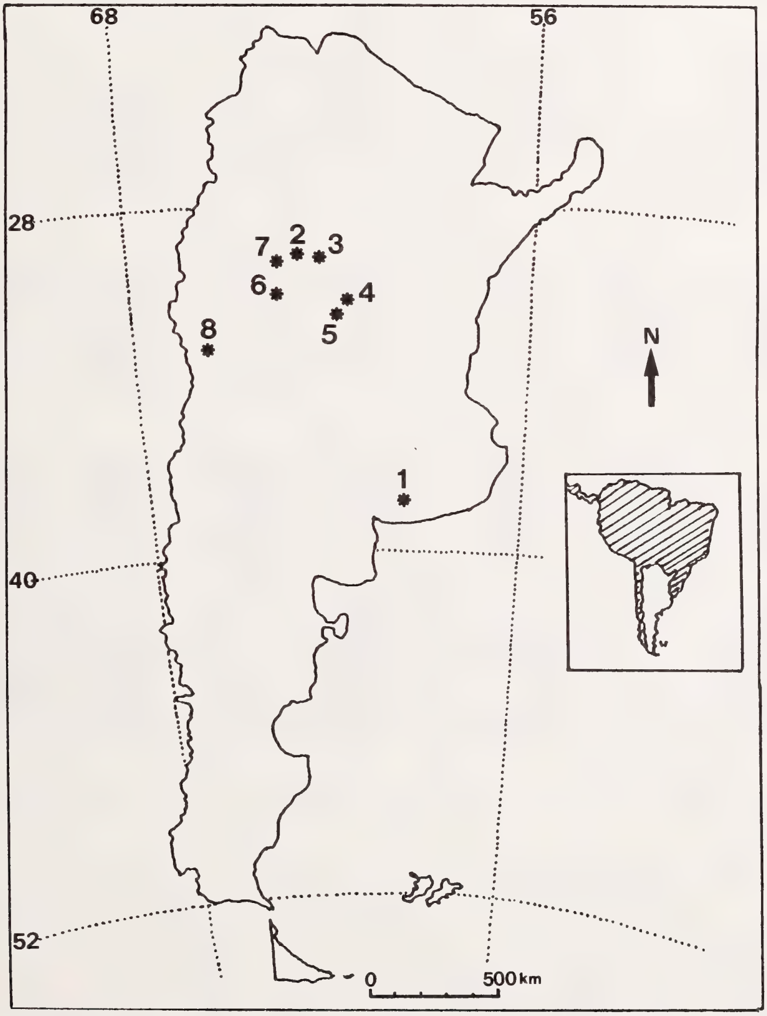

Fig. 1. Map showing the localities where specimens of *G. griseoflavus* were collected. 1: Chasicó; 2: La Carrera; 3: Deán Funes; 4: Santiago Temple; 5: Laguna Larga; 6: General Belgrano; 7: Salicas; 8: Divisadero Largo

Table 1. **Numbers of specimens of the different karyomorphs of *G. griseoflavus* collected in each locality**

Locality	42	41	38	37	36	35	34
1. Chasicó	–	–	12	9	4	–	–
2. La Carrera	1	–	1	4	1	–	–
3. Deán Funes	4	1	–	–	1	–	–
4. Santiago Temple	7	–	–	–	–	–	–
5. Laguna Larga	4	–	–	–	–	–	–
6. General Belgrano	6	–	–	–	–	–	–
7. Salicas	–	–	1	1	2	–	–
8. Divisadero Largo	–	–	–	–	4	2	1

Results

Robertsonian fusions

The 2n = 42 karyomorph comprises twenty pairs of autosomes (Fig. 2a). Chromosomes 1–18 are acrocentric gradually decreasing in size (large to small). The pair 19 is a medium sized submetacentric and pair 20 is a small submetacentric. In some animals chromosome 4 can be submetacentric (see below pericentric inversions). The X is a large submetacentric and the Y is a small acrocentric chromosome.

The 2n = 38 karyomorph shows fourteen pairs of acrocentric and two additional pairs of large submetacentric autosomes. These features constitute the main difference to the 2n = 42 karyomorph (Fig. 2b).

The G-banding pattern analysis of 2n = 42 and 2n = 38 karyomorphs allowed us to conclude that the two large submetacentric pairs observed in 2n = 38 animals resulted from RFs between the acrocentric chromosomes 15/17 and 16/18 pairs of 2n = 42 specimens (RF15–17 and RF16–18, respectively) (Fig. 2, Tab. 2).

It was previously proposed that the very large submetacentric chromosome of the 2n = 37 karyomorph was produced by a RF occurring in the 2n = 38 karyomorph. This assumption was based on morphological chromosomal comparisons between these karyomorphs and on the presence of one trivalent in diakinesis-metaphase I of 2n = 37 males. We identified by G-band comparison that the RF involves autosomes 1 and 6 (RF1–6) (Figs. 2, 3a, Tab. 2). RF1–6 is also present as heterozygous in the 2n = 41 karyomorph and as homozygous in the 2n = 36 karyomorph (Tab. 2, Fig. 3b). Diakinesis-metaphases I of 2n = 36 males showed 17 bivalents plus a symmetrical very large sized RF1–6 bivalent (Fig. 3e).

In the 2n = 35 karyomorph there was a decrease of two acrocentric and the appearence of one very large submetacentric chromosome produced which according to G-banding arose by centric fusion of autosome 2 and 5 (RF2–5) (Tab. 2). Diakinesis-metaphases I of

Table 2. **Different Robertsonian fusions found in each karyomorph of *G. griseoflavus***

2n	RF1–6	RF2–5	RF15–17	RF16–18
42	–	–	–	–
41	Ht	–	–	–
38	–	–	Hm	Hm
37	Ht	–	Hm	Hm
36	Hm	–	Hm	Hm
35	Hm	Ht	Hm	Hm
34	Hm	Hm	Hm	Hm

(–) = absence of RF.

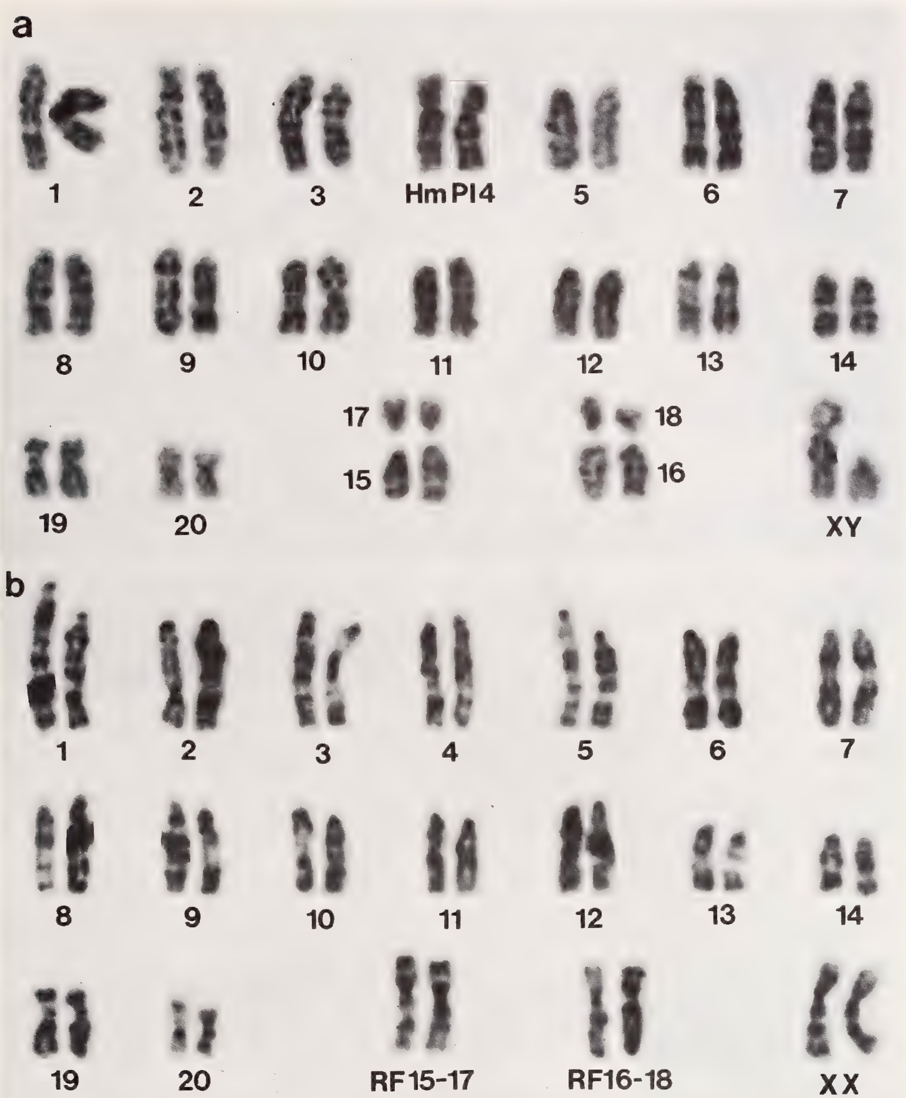

Fig. 2. G-banded karyotypes with 2n = 42 (a) and 2n = 38 (b) of *G. griseoflavus*. HmPI = homozygous pericentric inversion

2n = 35 specimens showed 15 bivalents, one very large bivalent (homozygous RF1–6) and one trivalent, which is formed by chromosomes RF2–5, 2 and 5 (Fig. 3f).

In the 2n = 34 karyomorph the RF2–5 was homozygous (Fig. 3c, Tab. 2).

Pericentric inversions

In our survey, we found two autosomal acrocentric pairs that underwent pericentric inversion (PI), giving rise to submetacentric elements. G-band analysis showed that this rearrangement involved chromosomes 4 and 13 (PI4 and PI13, respectively) (Figs. 2a, 3d).

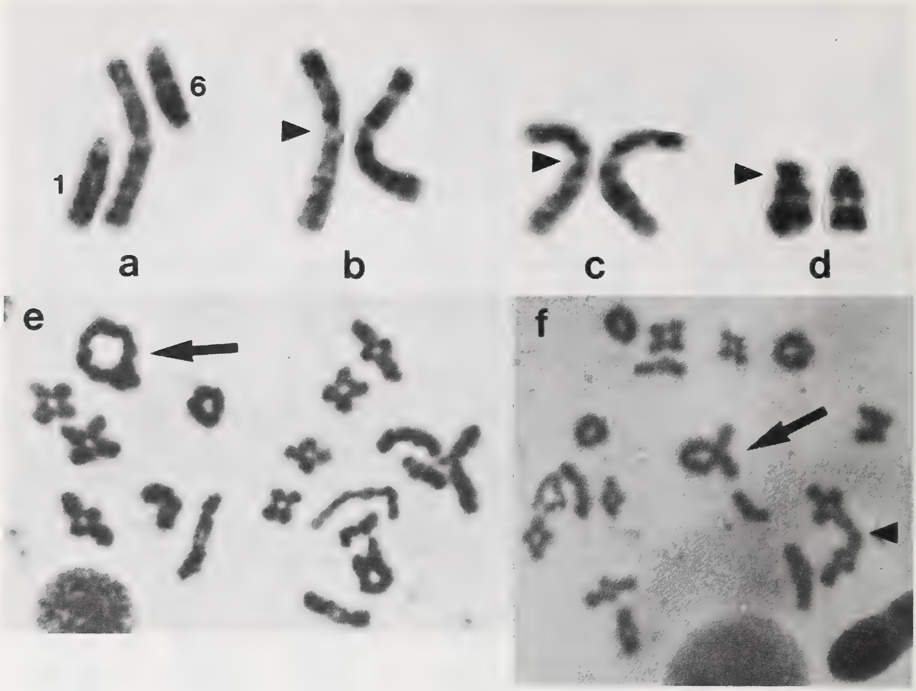

Fig. 3. a: G-banded RF1–6 and its acrocentric homologues (1 and 6 autosomes) from a 2n = 37 karyomorph; b: G-banded RF1–6 chromosome pair from a 2n = 36 karyomorph; c: G-banded RF2–5 chromosome pair from a 2n = 34 karyomorph; d: Heterozygous pericentric inversion of pair 13 from a 2n = 37 karyomorph; e–f: Diakinesis-metaphaseI figures from 2n = 36 (e) and 2n = 35 (f) karyomorphs. The arrows point to the very large RF-bivalent; the arrow head points to the trivalent

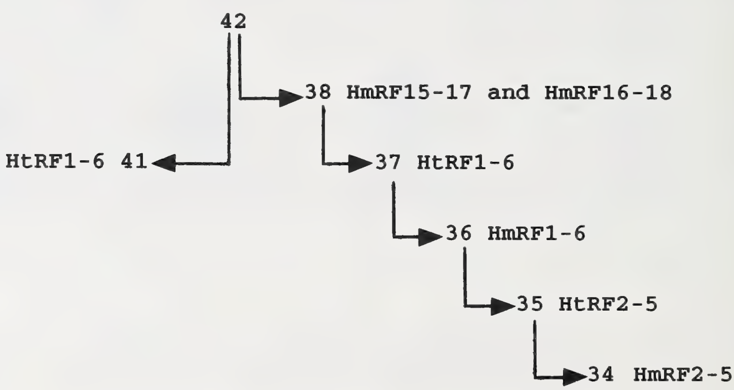

Fig. 4. Sequence of Robertsonian fusions explaining the karyotypic divergence of *G. griseoflavus*

The PI4 was found in 2n = 42, 38, 37 and 36 karyomorphs. The PI13 was found in 2n = 38, 37 and 36 karyomorphs. Within a population both PIs may show a homozygous or heterozygous state or even be absent.

Discussion

The phyllotine rodent *Graomys griseoflavus* exhibits a high degree of chromosomal polymorphisms produced by two pericentric inversions and four Robertsonian fusions. Cytogenetic findings suggest that the latter rearrangements occurred non-randomly and can be summarized as follows: a. the RF15–17 and RF16–18 (present in 2n = 38–34 complex) were always found in a homozygous state; b. all 2n = 37–36 individuals were heterozygous and homozygous respectively for RF1–6; c. all 2n = 35–34 animals examined were homozygous for RF1–6 and heterozygous and homozygous respectively, for RF2–5. These findings suggest a sequencial occurrence of Robertsonian fusions. Thus, HmRF15–17 and HmRF16–18 (uncertain who was first) were followed by HtRF1–6, HmRF1–6, HtRF2–5 and HmRF2–5. On these grounds, we propose a sequence of Robertsonian events that lead to the karyotypic divergence observed, with the 2n = 42 as the common ancestral karyomorph (Fig. 4). This assumption agrees with the view of GARDNER and PATTON (1976) that karyotypic evolution in Neotropical cricetids decreases the chromosomal number via Robertsonian fusions.

To explain the karyotype divergence from 2n = 42 to 2n = 38 we assumed the existence of the 2n = 41, 40 and 39 karyomorphs. At least, the 2n = 41 and 39 individuals should be heterozygous for RF15–17 or RF16–18. Thus far, in fifty-one wild animals studied only individuals homozygous for these Robertsonian fusions were found. Thus, we assumme that the heterozygous animals may be not viable or that its frequency is low. To test these hypotheses we performed experimental crosses to asses the segregation of Robertsonian chromosomes. In matings between 2n = 42/41, 2n = 38/37, 2n = 38/36 and 2n = 37/37 individuals the F1 and F2 progenies showed normal meiosis and RF15–17, RF16–18 or RF1–6 segregating in a Mendelian fashion. On the other hand, when matings between 2n = 42/38 and 2n = 42/37 individuals were tried under the same laboratory breeding conditions, no offsprings were obtained. Probably, the unsuccesful breedings were due to the inviability of heterozygous RF15–17 and RF16–18 embryos.

There is evidence that Robertsonian fusions may be involved in speciation processes only when they cause reproductive failure, e. g. in the case of meiosis nondisjunction (KING 1987). In *Graomys griseoflavus* the inviability of heterozygous RF15–17 and/or RF16–18 products may produce reproductive isolation of 2n = 42–41 and 2n = 38–37–36 (and probably also 2n = 35–34) karyomorphs, while heterozygous RF1–6 and RF2–5 (this latter always present together with HmRF1–6) would not induce reproductive isolation.

According to the remarkable chromosomal polymorphism described in *Graomys griseoflavus* we suggest that this species is evolving actively and therefore represents an interesting model for speciation and chromosomal evolutionary studies.

Acknowledgements

We thank to Dr. NOEMÍ GARDENAL for providing some specimens included in this work and to ANIBAL RAMOS for the technical assistance. Our appreciation go to Dr. N. O. BIANCHI and Dr. K. FREDGA for critical reading and suggestions on this manuscript. This paper was supported by CONICET grant PIDs 3085300/85 to R. W. and 3066400/88 to L.V.R.

Zusammenfassung

Cytogenetische Analysen von Autosomen-Polymorphismen bei Graomys griseoflavus (Rodentia, Cricetidae)

Graomys griseoflavus aus Südamerika wurden an acht verschiedenen Orten gefangen und cytogenetisch untersucht. In diesen Populationen wurden Karyotypen mit folgenden Chromosomenzahlen gefunden: 2n = 42, 41, 38, 37, 36, 35 und 34. Diese numerischen Karyotypvariationen werden auf Robertsonsche Fusionen (RFs) zurückgeführt. Es wurden vier verschiedene RFs beschrieben, die acht akrocentrische Autosomen als Fusionspartner betreffen. Weiterhin wurden pericentrische Inversionen

an zwei verschiedenen Autosomen festgestellt. Die zahlenmäßigen Karyotypvariationen werden durch aufeinanderfolgende RFs erklärt, wobei als Ausgangskaryotyp der mit 2n = 42 postuliert wird.

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Authors' addresses: Andrés Zambelli and Lidia Vidal-Rioja, IMBICE, CC403 (1900) La Plata, Argentina; Ricardo Wainberg, Cátedra de Biología General, Departamento de Ciencias Biológicas, Facultad de Ciencias Exactas 47 y 115, Universidad Nacional de La Plata, (1900) La Plata, Argentina

Z. Säugetierkunde 59 (1994) 21–26

ISSN 0044-3468

Zur Altersstruktur von *Apodemus flavicollis* in einem Auwald an der mittleren Elbe

Von J. Haferkorn und M. Stubbe

Institut für Zoologie, Martin-Luther-Universität, Halle-Wittenberg, Deutschland

Eingang des Ms. 28. 1. 1993
Annahme des Ms. 21. 9. 1993

Abstract

Age structure of Apodemus flavicollis in a floodplain forest in the middle part of the river Elbe

Studied age structure of *Apodemus flavicollis* in a floodplain forest in the middle part of the river Elbe. Age was determined using the dry mass of crystalline lenses of the eye. There exists a relationship between age of animals and mass of lens. Three month old *A. flavicollis* had an average life expectancy of 3.8 months. The average age of the population was 6.6 months, however, this changed throughout the year with a maximum in April of 12.2 months and a minimum of 5 months in summer. The turnover rate during the course of the year was 86.6 %. Sex ratio was nearly balanced with a slight female bias.

The results indicate the typical high turnover rate and short life expectancy for small rodents.

Einleitung

Sichere Methoden zur Altersbestimmung bilden die Grundlage für die Erforschung der Struktur und des Umsatzes von Populationen. Bisher war die Ermittlung des Alters gefangener Gelbhalsmäuse nur begrenzt möglich. Aufgaben dieses Beitrages sind die Darstellung einer Methode zur Altersbestimmung gefangener Gelbhalsmäuse und darauf aufbauend Aussagen zur Altersstruktur.

Untersuchungsgebiet

Mit dem Lödderitzer Forst wurde ein naturnaher Auwald mit Hartholzauenbestockung ausgewählt. Das Gebiet gehört zum Biosphärenreservat „Mittlere Elbe" und liegt im Bundesland Sachsen-Anhalt.

Aufgrund des hohen technischen Ausbauungsgrades der Elbe und deren Nebenflüsse trat im Untersuchungsgebiet letztmalig im April 1988 Hochwasser auf. In den Totalreservaten werden heute keine forstwirtschaftlichen Maßnahmen mehr durchgeführt, frühere Eingriffe sind im Bestockungsbild noch sichtbar.

In der oberen Baumschicht dominieren *Quercus robur, Fraxinus excelsior, Tilia cordata* und partiell anthropogen begründet *Populus x canadensis*. Eine zweite Baumschicht ist mit *Acer campestre, Carpinus betulus, Tilia cordata* und vor allem *Ulmus minor* ausgebildet. Die in den meisten Waldbereichen gut strukturierte Strauchschicht setzt sich aus *Crataegus laevigata, Corylus avellana, Tilia cordata* und *Ulmus minor* zusammen. Typische Bodenpflanzen sind *Anemone nemorosa, Glechoma hederacea, Stellaria holostea, Carex brizoides* und *Impatiens parviflora*.

Material und Methode

Die Untersuchungen wurden von August 1989 bis Oktober 1991, mit 21 über den gesamten Jahresverlauf verteilten Fangperioden, durchgeführt. Das Stellen der Schlagfallen erfolgte nach der Fangquadratmethode von Sykora (1978). Die Fallen wurden täglich kontrolliert und nachbeködert, als Köder kamen Brot und Speck zum Einsatz.

Bei allen gefangenen Tieren (n = 268) wurde der Schädel freipräpariert. Unter dem Stereomikro-

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skop erfolgte bei ca. 25-facher Vergrößerung eine Einstufung in sechs Zahnabnutzungsklassen nach Steiner (1968). Ferner wurden die Bulbi beider Augen herauspräpariert und mit einem Skalpell angeschnitten. Unter leichtem Druck kamen Glaskörper und Augenlinse hervor, deren Trennung durch Drehungen und leichten Druck erfolgte. Die Augenlinsen wurden 24 Stunden in 10%igem Formalin fixiert und in 4%igem Formalin ca. 14 Tage gelagert, nach der Methode von Morris (1972). Die Trocknung erfolgte im Exikator auf Blaugel im Trockenschrank bei ca. 80 °C über 48 Stunden. Beide Augenlinsen eines Individuums wurden paarweise auf 0,1 mg genau gewogen. Die Wägungen wurden in Abständen zweimal wiederholt, die Daten dieser drei Messungen wurden gemittelt.

Über die Relation der Linsenmasse mit dem Alter der Tiere wurde eine Eichkurve erstellt, die zur Alterseinstufung des Fangmaterials diente. Tiere bekannten Alters wurden in Standardversuchstierkäfigen aus PVC-Schalen und Gitteraufsätzen mit den Maßen 50 × 30 × 19 cm auf Spänen gehalten. Als Unterschlupf dienten umgestülpte Blumentöpfe mit ausgebrochenen Rändern. Wasser und Mäuse- bzw. Rattenpellets standen ad libitum zur Verfügung. Dreimal wöchentlich bekamen die Tiere Frischfutter, meist Äpfel. Die Haltung erfolgte bei einer Temperatur von ca. 20 °C unter einem konstanten Langtaglichtregime (L:D = 16:8). Insgesamt wurden Linsenpaare von Tieren mit einem Alter von 11 Wochen (n = 22), 4 Monaten (n = 12), 6 Monaten (n = 10), 8 Monaten (n = 7), 10 Monaten (n = 10), 16 Monaten (n = 9) und 18 Monaten (n = 3) verwendet. Statistische Unterschiede wurden mit dem parameterfreien, univariaten Mann Whitney U-Test geprüft.

Ergebnisse

Bei *A. flavicollis* wurde eine funktionale Abhängigkeit der Augenlinsenmasse vom Alter der Tiere registriert (Abb. 1). Die Gleichung der Regression auf y lautet $y = 10{,}786 \ln x - 7{,}638$ ($r = 0{,}989$). Die Augenlinsentrockenmassen der Tiere, getrennt in Zahnabnutzungsklassen nach Steiner (1968), unterschieden sich in jedem Falle signifikant (I–VI: U = 4,774; 8,147; 9,74; 6,625; $\alpha = 0{,}0001$/U = 3,102; $\alpha = 0{,}005$), obwohl sich die Werte besonders in den höheren Zahnabnutzungsklassen beträchtlich überschnitten (Tab. 1).

Einen Überblick über die Altersstruktur vermittelt die Lebenstafel (Tab. 2). In ihr wurden Tiere ab einem Alter von drei Monaten berücksichtigt, da Jungtiere in Freilandfängen in ihrer Nestlingsperiode und kurz danach unterrepräsentiert erfaßt werden. Die mittlere Lebenserwartung stieg vom dritten zum fünften Lebensmonat und sank dann mehr oder weniger kontinuierlich mit zunehmendem Alter. Jungtiere mit einem Alter von drei Monaten hatten eine mittlere Lebenserwartung von 3,8 Monaten.

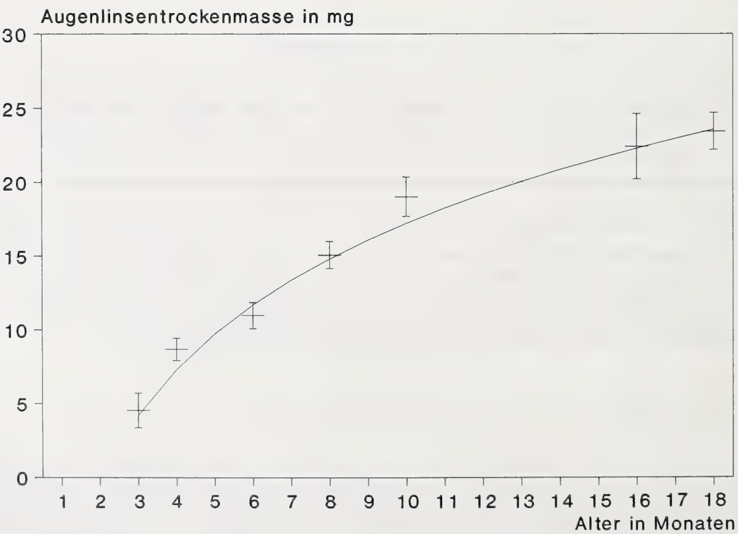

Abb. 1. Augenlinsentrockenmassen in Abhängigkeit vom Alter der Tiere

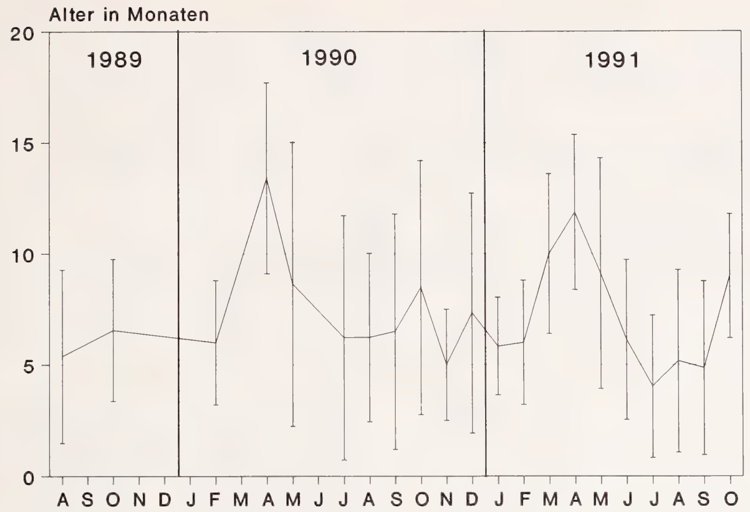

Abb. 2. Das mittlere Alter aller gefangenen *A. flavicollis* im Auwald (Balken gibt Standardabweichung an)

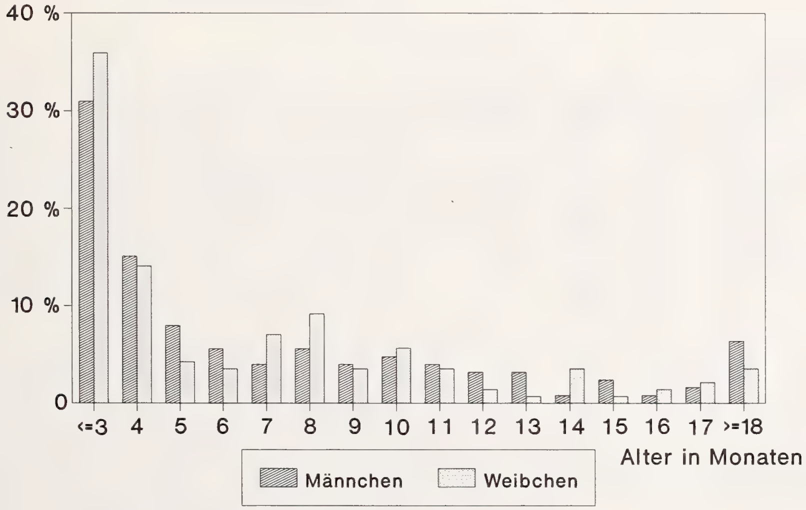

Abb. 3. Der prozentuale Anteil einzelner Altersklassen am Populationsaufbau

Im gesamten Fangmaterial betrug das durchschnittliche Alter aller Tiere 6,6 Monate. Vom Spätherbst bis zum Beginn der neuen Reproduktionsperiode stieg das mittlere Alter der Population mit Maximalwerten im April 1990 von 13,4 Monaten bzw. im April 1991 von 11,9 Monaten (Abb. 2). Minimalwerte des mittleren Alters der Population wurden jeweils im Sommer mit vier bis sechs Monaten registriert. Auffällig ist das geringe mittlere Alter von fünf Monaten im November 1990, welches auf sechs gefangenen Individuen basiert. Der Anteil vorjähriger Tiere in der Population sank bis August auf 17 bis 28 %. Letztmalig wurden Tiere nach einer Überwinterung im darauffolgenden Jahr im Dezember gefangen. Der Populationsumsatz fand im Verlaufe eines Jahres zu 86,6 % statt und ist mit eineinhalb bis zwei Jahren abgeschlossen.

Tabelle 1. **Mittlere Augenlinsentrockenmassen ($\bar{x}$) und mittleres Alter ($\bar{x}$) im Verhältnis zu den Zahnabnutzungsklassen**
(s = Standardabweichung, min. = minimales Alter, max. = maximales Alter)

Zahnabnutzungsklasse	n	Augenlinsen-TM $\bar{x}$	Augenlinsen-TM s	Alter in Monaten $\bar{x}$	Alter in Monaten min.	Alter in Monaten max.
I	11	2,69	0,35	≦ 2	≦ 2	≦ 2
II	50	5,74	1,83	3	≦ 2	4
III	103	10,07	2,95	4	≦ 2	9
IV	58	16,95	2,15	8	5	14
V	34	21,83	3,07	14	11	≧ 18
VI	12	24,62	1,95	≧ 18	14	≧ 18

Tabelle 2. **Lebenstafel für *Apodemus flavicollis***
(I: Zahl der lebenden Tiere bezogen auf 1000 Individuen, d: Zahl der sterbenden Tiere innerhalb der Altersklasse, q: Sterberate in % innerhalb der Altersklasse, e: mittlere Lebenserwartung in Monaten für Tiere zu Beginn der Altersklasse)

Alter in Monaten	I	d	q	e
≧ 3	1000	335	33,5	3,84
4	665	146	22,0	4,77
5	519	60	11,6	5,11
6	459	45	9,8	4,78
7	414	56	13,5	4,3
8	358	75	20,9	3,97
9	283	37	13,1	4,02
10	246	52	21,1	3,63
11	194	37	19,1	3,6
12	157	22	14,0	3,44
13	135	19	14,1	3,0
14	116	22	19,0	2,5
15	94	15	16,0	2,08
16	79	11	13,9	1,48
17	68	19	27,9	0,72
18	49			

Insgesamt wurde ein Männchenanteil von 48 % registriert. Das Zahlenverhältnis der Geschlechter war in den einzelnen Altersklassen mehr oder weniger ausgeglichen. Bei Jungtieren mit einem Alter bis zu drei Monaten deutet sich ein leichter Weibchenüberschuß an (Abb. 3).

Diskussion

Analysen zur Altersstruktur von *A. flavicollis* fehlen, da bisher keine genaue Altersbestimmung möglich war. Für die nahe verwandte Art *A. sylvaticus* liegen bereits zwei Untersuchungen vor, die sich mit dem Zusammenhang der Linsenmassen und dem realen Alter der Tiere befaßten (Gurnell und Knee 1984; Quere und Vincent 1989). Bei Freilandfängen von *A. flavicollis* bestimmten Nabaglo und Pachinger (1979) die Augenlinsentrockenmassen. Da ihnen das Alter der Tiere nicht bekannt war und eine Eichkurve fehlte, konnten sie die Linsenmassen nur mit dem Abkauungsgrad der Backenzähne vergleichen. Der Abkauungsgrad der Zähne ist im starken Maße abhängig von der Härte der aufgenommenen Nahrung, besonders vom Anteil der Oxalatkristalle im Pflanzenmaterial. Dadurch nutzen sich die Zähne sehr unterschiedlich ab, beispielsweise schwankte das anhand der Augenlinsen ermittelte Alter der Tiere aus der dritten Zahnabnutzungsklasse nach Steiner (1968) zwischen zwei und neun Monaten. Auf die Ungenauigkeit von Altersabgrenzungen bei *A. flavicollis* anhand der Zahnabnutzung wiesen schon Adamczewska (1959) und Eichstädt (1987) hin.

Lebendfänge von *A. flavicollis* mit individueller Markierung führten Radda et al. (1969) in Niederösterreich, Ylönen et al. (1991) in einem Feldgehölz bei Halle und Hugo (1990) im Nationalpark Berchtesgaden durch. Das Höchstalter markierter *A. flavicollis* gaben Radda et al. (1969) mit 18 Monaten und Hugo (1990) mit 22 Monaten an. In der Elbaue betrug der Anteil von *A. flavicollis* mit einem Mindestalter von 18 Monaten noch 4,9 %.

Die mittlere Lebenserwartung von Jungtieren gaben Radda et al. (1969) zwischen 3,5 und 3,9 Monaten an, für die Elbaue wurde ein ähnlicher Wert errechnet (3,8 Monate).

Entsprechend dem Fortpflanzungsgeschehen schwankte das Durchschnittsalter der Population im Jahresverlauf mit einem Maximum im April zu Beginn der Reproduktionsperiode. Die darauffolgende starke Verjüngung wird bedingt durch die Natalität und den Verlust von Alttieren, da bis zum Frühsommer viele vorjährige Tiere absterben. Auffällig ist das geringe Durchschnittsalter der Population im November 1990. In dem Jahr reproduzierte *A. flavicollis* bis Ende September nach einer geringen Fortpflanzungsrate im trockenen Hochsommer (Haferkorn 1992). Möglicherweise verursachten die Septemberwürfe eine zweite Populationsverjüngung im Spätherbst. Fangbedingte Abweichungen von realen Verhältnissen können allerdings nie ausgeschlossen werden. Zejda (1976) stellte die Altersgruppierung von *A. flavicollis* in einem südmährischen Auwald dar und erklärte Unterschiede in der Altersstruktur zwischen den einzelnen Untersuchungsjahren mit dem Zusammenspiel von der Dauer und der Intensität der Fortpflanzungsperiode.

Flowerdew (1985) beschreibt für die Art dichteabhängige Überlebensraten, die mit geringeren Abundanzen steigen. Verbunden mit einem hohen Reproduktionsstoß müßten die Populationen in partiell überfluteten Auwäldern die Möglichkeit zur schnellen Besiedlung trockenfallender Waldbereiche haben. Für den Lödderitzer Forst konnte diese Vermutung in den Hochwasserjahren 1987 und 1988 für *Clethrionomys glareolus*, nicht aber für *Apodemus flavicollis* bestätigt werden (Haferkorn et al. 1991).

Zusammenfassung

Die Altersstruktur von *Apodemus flavicollis* wurde in einem Auwald an der mittleren Elbe untersucht. Zwischen dem Alter der Tiere und der Augenlinsentrockenmasse existiert ein positiv korrelativer Zusammenhang, der zur Altersbestimmung genutzt wurde. Drei Monate alte *A. flavicollis* hatten eine mittlere Lebenserwartung von 3,8 Monaten. Das Durchschnittsalter der Population betrug 6,6 Monate und schwankte im Jahresverlauf mit einem Maximum im April von 12,2 Monaten und einem Minimum von fünf Monaten im Sommer. Der Populationsumsatz im Zeitraum eines Jahres betrug 86,6 %. Das Zahlenverhältnis der Geschlechter war relativ ausgeglichen mit einem leichten Weibchenüberschuß.

Die Resultate zeigen die für Kleinnager typische hohe Populationsumsatzrate, verbunden mit einer geringen individuellen Lebenserwartung.

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Anschriften der Verfasser: Dr. Jörg Haferkorn, Umweltforschungszentrum Leipzig-Halle GmbH, Sektion Biozönoseforschung, Hallesche Str. 44, D-06246 Bad Lauchstädt; Prof. Dr. Michael Stubbe, Institut für Zoologie Martin-Luther-Universität, Domplatz 4, Postfach Universität, D-06099 Halle (Saale), BRD

Z. Säugetierkunde 59 (1994) 27–41

ISSN 0044-3468

Island rodents: a new species of *Octodon* from Isla Mocha, Chile (Mammalia: Octodontidae)

By R. Hutterer

Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany

Receipt of Ms. 10. 2. 1993
Acceptance of Ms. 22. 3. 1993

Abstract

A hitherto unknown species of *Octodon* occurs on Isla Mocha, a small coastal island in the Valdivian rainforest zone of central Chile. The new Pacific degu (*Octodon pacificus* n. sp.) exhibits characters such as soft and long fur, long and poorly tufted tail, homodont upper dentition, barely reduced third lower molars, broad and asymmetrical teeth with long reentrant folds full of cement, all of which are considered as plesiomorphic for the genus. It is suggested that geographic isolation led to the preservation of primitive characters. The new species probably represents the sister taxon of *Octodon bridgesii,* one of the three mainland species currently known from Chile and Argentina. The phylogenetic significance of the new degu is discussed.

Introduction

Hystricognath rodents of the family Octodontidae occur in west-central South America, from where six genera *(Aconaemys, Octomys, Octodon, Octodontomys, Spalacopus, Tympanoctomys)* with ten species are known from Bolivia, Chile and Argentina (Pearson 1984; Contreras et al. 1987; Mares and Ojeda 1982; Gallardo and Reise 1992). The systematic status and the contents of the family are rather controversial as no striking synapomorphies are known to characterize the group (Glanz and Anderson 1990); some authors include the Ctenomyidae (Reig 1970, 1986; Reig and Quintana 1991), others the Abrocomidae (Ellerman 1940).

Confusion also exists at the species level. Gallardo and Reise (1992) have recently demonstrated that the genus *Aconaemys* comprises three species, not one or two, as previously thought. Three species are generally accepted in the genus *Octodon: O. degus* (Molina, 1782), *O. bridgesii* (Waterhouse, 1844), and *O. lunatus* Osgood, 1943 (Osgood 1943; Mares and Ojeda 1982; Patterson and Feigl 1987; Reise and Venegas *S.* 1987; Gallardo 1992; Redford and Eisenberg 1992). Contreras et al. (1987) questioned the validity of *O. lunatus* on morphological grounds but the form has a distinctive karyotype (Spotorno et al. 1988) and certainly is a valid species. However, our knowledge on the taxonomy, distribution and ecology of this genus is far from being complete, as this report will show. New material already collected in 1959 from a small island off central Chile demonstrates the existence of a fourth species of *Octodon.* Its characters considerably enlarge the morphological diversity of the genus. The new degu is named and described below and its significance discussed in the context of the family.

Material and methods

The specimens studied are stored in the collections of the Museum Alexander Koenig, Bonn (ZFMK), the Staatliches Museum für Naturkunde Stuttgart (SMNS), the Senckenberg-Museum Frankfurt (SMF), and the collection of W. von Koenigswald, Paleontological Institute, University of Bonn (VKB). The following specimens were used for illustrations and for comparison: *Octodon degus,* 9

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(ZFMK 86.89, 86.701–3, 87.82, 87.361, 88.37; SMNS 1113, 33771), *O. bridgesii,* 9 (ZFMK 88.63, 88.83, 92.309, 92.382; SMNS 534; SMF 11037; VKB 972), *O. lunatus,* 2 (SMNS 42960; SMF 862), *O. sp.,* 4 (ZFMK 92.383–6), *Aconaemys fuscus,* 1 (ZFMK 88.59), *Spalacopus cyaneus,* 1 (ZFMK 92.310). Other sources of information were the descriptions and figures in Thomas (1920), Ellerman (1940), Wood (1949, 1974), Walker et al. (1964), Landry (1970), Reig (1970), Woods and Boraker (1975), Glanz and Anderson (1990), Nowak (1991), Reig and Quintana (1991), and de Santis et al. (1991). The terminology of the skull and the teeth follows Wood and Wilson (1936) and Woods and Howland (1979). All measurements are in millimetres. A note is required about the use of the name *Aconaemys* in this report. According to Reig (1986) the genus *Pithanotomys,* based on a fossil, has priority over *Aconaemys.* However, evidence which the author announced to be presented in a forthcoming paper was never published except for the same statement plus one figure of upper and lower dentition in Reig and Quintana (1991). Although the similarity between the molars of the extant *Aconaemys fuscus* and the Pliocene *Pithanotomys columnaris* is striking, the shape and structure of the skull has not been described. I therefore refrain from following Reig and Quintana (1991) until a thorough comparison of both extant and fossil forms has been published.

Results and discussion

Octodon pacificus, new species

Holotype: ZFMK 92.384, skin and skull of an adult female, collected by Francisco Behn on 16 January 1959, field number L 6. The skin is in good condition, the cranium (Fig. 2) lacks the occipital and the bullae; the mandible is complete.

Paratypes: Skins and skulls of another adult female (ZFMK 92.383; Fig. 1) and of two juveniles (ZFMK 92.385–6), collected between 11 and 24 January 1959 by F. Behn.

Measurements: See tables 1 to 3.

Type locality: Isla Mocha (38°22′ S, 73°55′ W), Arauca Province, Chile. Mocha Island is situated 31 km off the coast; its maximum extension from north to south is 13 km, and 5–7 km from west to east. The centre of the island forms a plateau of about 20 square kilometres which is almost entirely covered by myrtle forest (Mrs. Erika Behn, in litt.). Two peaks ascend to an altitude of 323 m in the north and 390 m in the south of the island. A lake is on top of the hills. Valleys run down from these peaks to the eastern coast. Large meadows cover the coastal plains of the island. Dr. Behn did not specify where he collected the small mammals but a recent map shows two airstrips on the eastern side of the island and one of them may have been the meadow where his expedition landed and camped. Bullock (1935) described the island as a hilly plateau covered with virgin forest, almost inacessable except where the inhabitants cut tracks into the forest. A short description of the island and its vegetation is also provided by Almeyda Arroyo (1955). Translated from Spanish it reads: “To the eye of the seaman Mocha Island presents a beautiful green aspect: the hills up to the peaks and the slopes towards the sea are covered with large trees, providing easy access to wood.” Isla Mocha is near the northern limit of the Valdivian rainforest zone, as outlined by Osgood (1943). Rocks and sediments of the island are of Miocene, Pliocene and Quaternary ages (Tavera and Veyl 1958).

Diagnosis: Larger and heavier than the three other species of *Octodon;* fur uniformly dark brown washed with orange, hairs soft and long; tail long (77 % of head and body length) with inconspicuous tuft. Skull long, particularly the diastema; zygomatic arches wide in dorsal and straight in lateral view; zygomatic process of squamosal inserting very high; superior jugal process forming a characteristic spine. Upper cheek-teeth very broad and uniform, the long reentrant folds filled with cement; lower cheek-teeth more or less homodont, their folds running strongly oblique and almost parallel; reentrant folds also cemented; the third lower molar is large and has the shape of an Arabic numeral 1.

Description: Although *Octodon pacificus* n. sp. is larger and heavier than *O. bridgesii, O. lunatus* and *O. degus* (Tab. 1), its body appears to be more slender (Fig. 1). The overall

colour of the pelage is brown-orange, with the orange tips being brighter on the hairs of the underside. The dorsal hairs are 22 mm long on average and very soft, scattered long guard hairs being up to 27 mm. The basal 80 % of the dorsal hairs are plumbous, their tips are brown-orange. The head of the animal is uniformly coloured; no pale eye rings are present. The relatively short dark ears appear almost naked, bearing only very fine short hairs. No white or yellow ear tufts exist. The snout bears about 30 vibrissae, some of which are black and others white. The forefeet have 4 digits with claws and a tiny pollex with a very reduced nail. Their dorsal surfaces are covered with greyish-brown hairs; they turn to white at the outer edge of each forefoot. The ventral surfaces are naked and show a granulation which is typical for the genus. Each palmar surface has three interdigital and two palmar pads. The hairs on the dorsal surfaces of the hindfeet are creamy-brown. A group of long and stiff white hairs sit on top of each digit. Finely granulated skin covers the space between the five interdigital and two plantar pads on the ventral surfaces of the hindfeet. The tail is long (77 % of head and body length), thinly haired, with the terminal 50 mm bearing a tuft of slightly longer and darker hairs. The more proximal part of the tail is brown on the dorsal and cream-brown on the ventral surface; the inconspicuous terminal tuft appears dark brown.

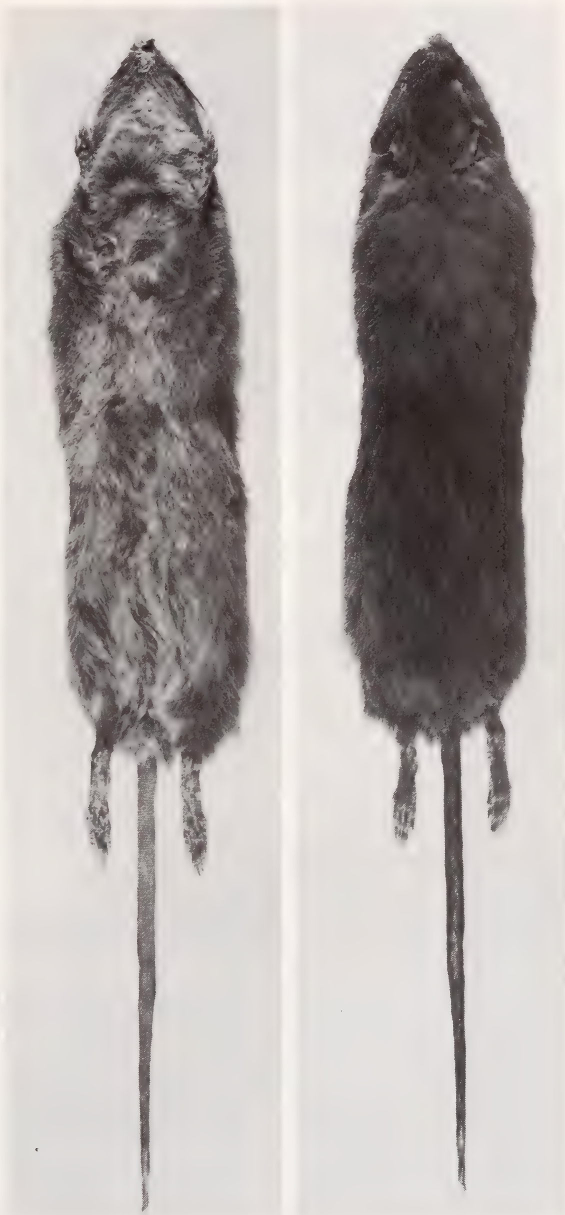

Fig. 1. Octodon pacificus n. sp., dorsal and ventral aspect of the skin of paratype ZFMK 92.383; total length of the specimen is 390 mm

The cranium of *Octodon pacificus* n. sp. is shown in Fig. 2. Unfortunately, the bullae and the occipital have not been preserved, due to the initial preparation of the animals in the style of a bird skin. The skulls were subsequently removed from inside the skins and

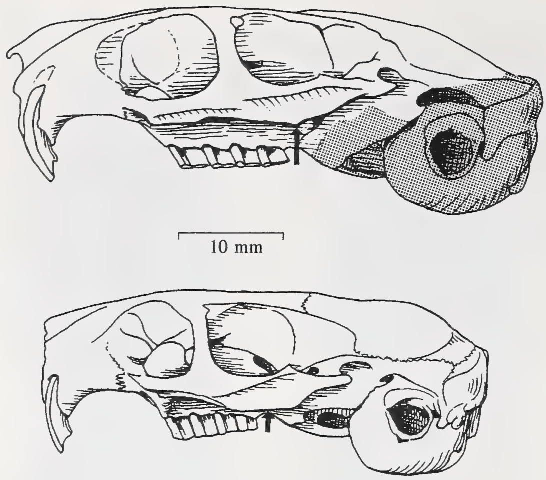

Fig. 2. Lateral view of a cranium of *Octodon pacificus* n. sp. (based on the holotype, missing parts of the shaded area reconstructed), and of a cranium of *O. degus* (below, adopted from Woods and Boraker 1975). Note the differences in size, diastema, infraorbital foramen, and the position of the inferior rim of the zygomatic arch (arrowed)

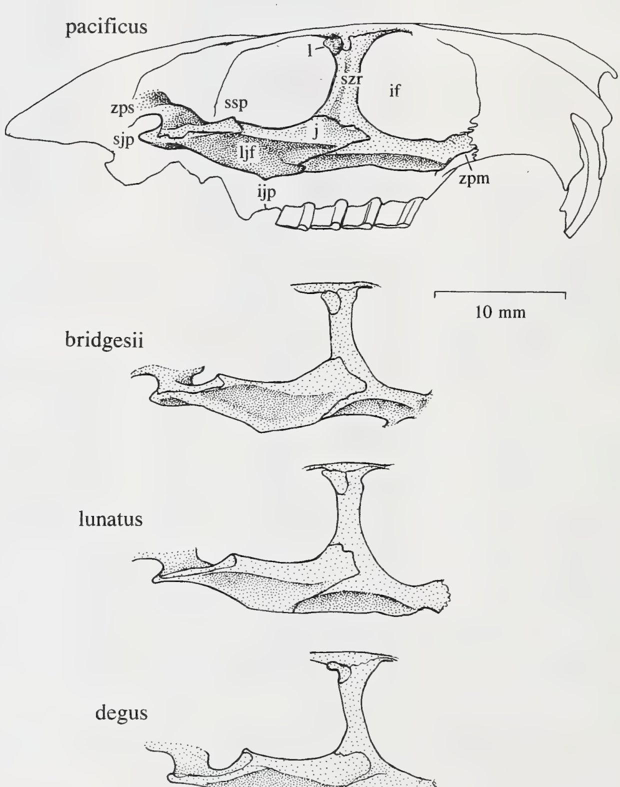

Fig. 3. A comparison of the zygomatic arch in the four species of *Octodon*. *if:* infraorbital foramen; ijp: inferior jugal process; j: jugal; l: lacrymal; ljf: lateral jugal fossa; sjp: superior jugal process; ssp: superior squamosal process; szr: superior zygomatic root; zpm: zygomatic process of maxillary; zps: zygomatic process of squamosal

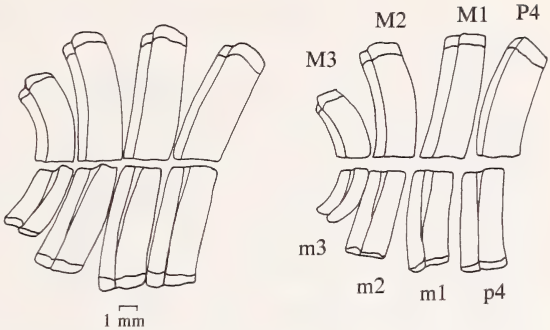

Fig. 4. Isolated left upper and lower molars of *Octodon pacificus* n. sp. (left side) and *O. bridgesii* in lingual view

the skins reworked as standard study skins in 1992. The skull is large and broad, with a long diastema, a large infraorbital foramen, and a broad interorbital constriction. The lateral ridges of the frontals form a thin, translucent roof which extends further than in the other species. The measurements for the zygomatic width of both adult specimens exceed all known measurements for the other species (Tab. 2); the same holds for the length of the nasals. The tips of the nasals project further than in the other species of the genus (Fig. 2). In its general configuration the skull of *Octodon pacificus* n. sp. resembles more that of *O. bridgesii.* In side view the zygomatic arch is diagnostic: its jugal-maxillary part is very straight, as is the upper rim of the lateral jugal fossa; the insertion of the zygomatic process of the squamosal is very high, leaving considerable space between the inferior jugal process and the upper molar row (Figs. 2, 3). The superior jugal process forms a characteristic spine, less developed in the other species of the genus. The superior zygomatic root points slightly obliquely in anterior direction, whereas this bone is upright or even points posteriorly in the other species (Fig. 3). The superior squamosal process is poorly developed, much less so than in *O. lunatus* and *O. degus.*

The upper incisors are thick and broad (Tab. 2) and their position is opisthodont; the anterior surfaces are stained orange, and the tips are deeply notched. The upper cheek-teeth are rootless (Fig. 4) and larger and especially broader than in the other species (Tab. 3, Figs. 5, 6). Both upper and lower teeth are more uniform in size and shape than in the other species (Fig. 4). In fact, the upper P4 to M3 show only minor differences in size, not in shape. All are highly asymmetrical with a heavy paracone and metacone and a long reentrant fold which is almost completely filled with cement (Fig. 6). The same is true for the lower cheek-teeth; here the two enamel folds run parallel to each other and strongly oblique. The third lower molar is somewhat simplified but keeps the size and aspect of the

Table 1. **External measurements and body mass of samples of *Octodon*; size data for species other than *pacificus* n. sp. taken from Redford and Eisenberg (1992), and body mass from Bozinovic (1992)**

	O. pacificus n. sp. holotype	paratype	*O. bridgesii* n3–4	*O. lunatus* n4–6	*O. degus* n64–75
Total length	380	390	323.0 250–370	360.0 328–382	266.5 200–307
Tail length	170	165	138.3 102–167	157.0 152–161	111.4 81–138
Hindfoot c.u.	40	42	38.5 34–40	40.7 40–42	35.5 31–40
Ear	20	20	22.0 20–23	28.0 –	24.7 19–31
Body mass (g)	290	290	176.1 (n23)	173.2 (n24)	195.0 (n52)

Table 2. **Cranial measurements of some specimens of *Octodon* spp.**

	O. pacificus n. sp.[1]		*O. bridgesii*[2]	*O. lunatus*[3]	*O. degus*[4]
Greatest length	[46.3]	–	41.8–44.8	46.5	43.3
Zygomatic width	25.9	25.3	23.7–23.9	23.8	23.9
Interorbital width	10.0	8.6	8.1– 9.0	9.1	10.3
Nasalia length	19.6	19.5	17.6	18.0	15.6
Nasalia width	5.9	5.6	5.1– 5.8	5.8	5.3
Diastema length	10.8	10.6	8.1– 9.9	8.7	8.8
Upper toothrow, crowns	10.3	10.9	9.5–10.0	9.3	9.5
Upper toothrow, alv.	11.1	11.3	9.6–10.6	10.7	10.1
Width P4–P4	7.8	8.2	6.5– 7.7	8.6	6.2
Width of both upper I1	4.0	4.2	3.1– 3.7	4.2	3.6

[1] holo-, paratype. – [2] 6 skulls (ZFMK, SMNS, VKB). – [3] SMNS 42960. – [4] ZFMK 86.701.

Table 3. **Width of upper (P4–M3) and lower (p4–m3) cheek-teeth of two adult specimens each of *Octodon pacificus* n. sp. (holo- and paratype), *O. bridgesii*, and *O. degus***

	O. pacificus n. sp.	*O. bridgesii*	*O.degus*
P4	2.82, 2.85	2.57, 2.50	2.04, 2.11
M1	2.57, 2.70	2.40, 2.29	1.96, 1.98
M2	2.67, 2.62	2.39, 2.31	1.99, 1.96
M3	2.34, 2.28	1.99, 1.84	1.79, 1.66
p1	2.26, 2.22	2.22, 2.30	1.85, 1.89
m1	2.27, 2.47	2.41, 2.24	1.93, 2.15
m2	2.30, 2.45	2.15, 2.16	1.76, 1.62
m3	2.05, 2.33	1.66, 1.74	1.50, 1.56

other molariform teeth. In occlusal view, this tooth resembles the Arabic numeral 1 (Fig. 6).

The mandible is larger and heavier than in the other species of the genus, as are the lower incisors. The condyloid process is particularly broad and heavy, corresponding to a large glenoid fossa of the squamosal, as may be inferred from the development of the posterior zygomatic root of the cranium (Fig. 3).

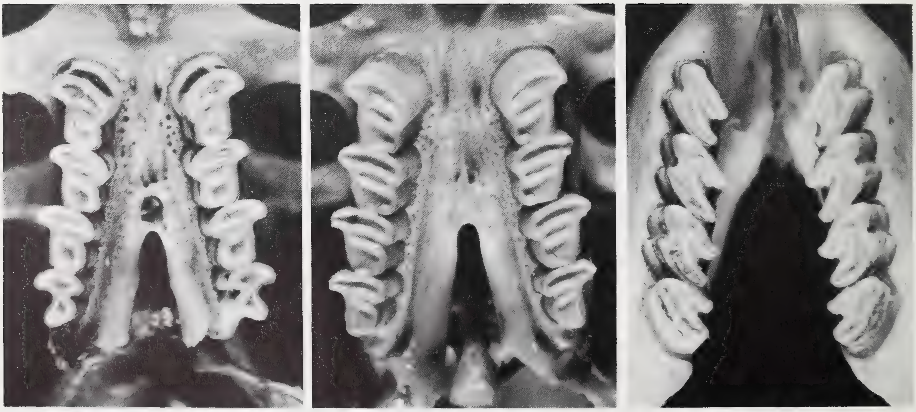

Fig. 5. Occlusal view of upper and lower molars. *Left: Octodon bridgesii* (ZFMK 88.63), *middle: O. pacificus* n. sp. (ZFMK 92.384), *right: O. pacificus* n. sp. (ZFMK 92.383); for measurements, see table 2

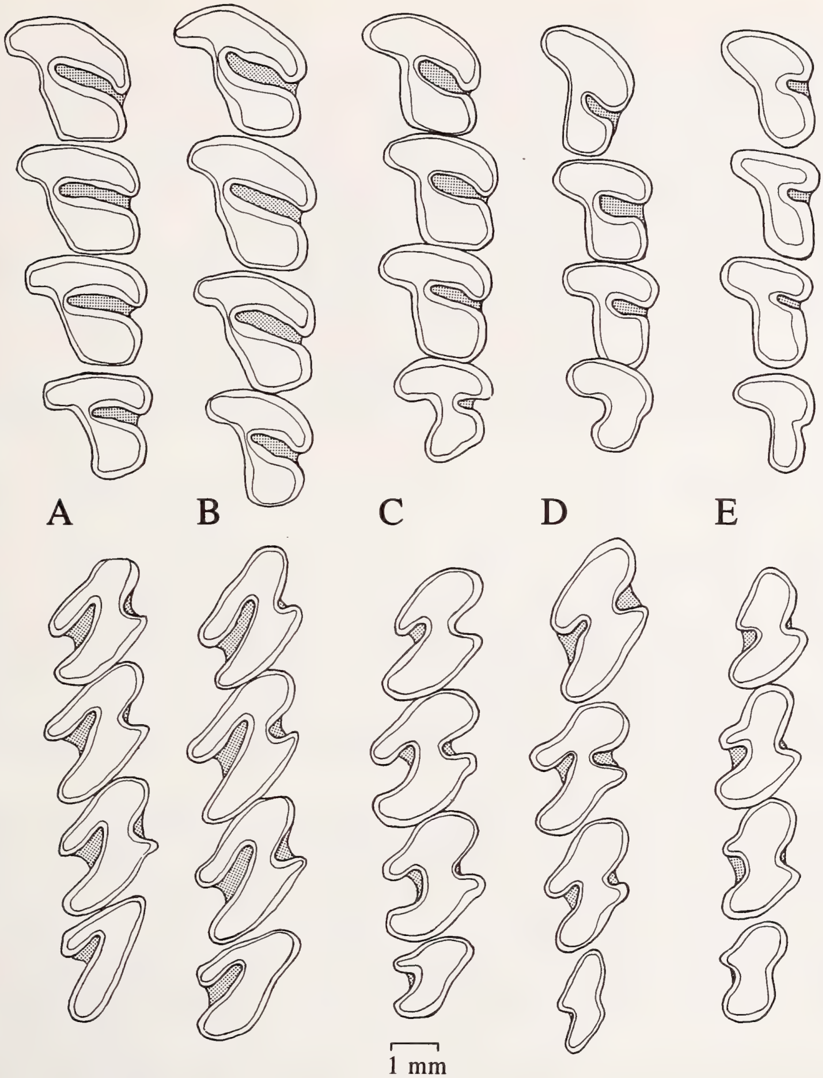

Fig. 6. Occlusal view of right upper and right lower molars of the four species of *Octodon.* A: *O. pacificus* n. sp. (holotype), B: *O. pacificus* n. sp. (paratype), C: *O. bridgesii* (ZFMK 88.63), D: *O. lunatus* (SMNS 42960), E: *O. degus* (ZFMK 86.701). The shading indicates cement

Notes on juveniles: As mentioned above, two juveniles were collected together with the two adult females. Their general appearance matches that of the adults, except the fur is duller. Especially the venter is more grey and not washed with orange. The weights of the young were 50 and 55 g, respectively, and the upper and lower third molar were not erupted. Their age may be estimated at two or three weeks. Assuming this age, they would have been born around the last week of December. Taking a gestation time of 90 days as in *Octodon degus* (Weir 1974), conception would have occurred in September of the previous year. This coincides with the reproduction period of *Octodon degus* near Santiago, Chile (Fulk 1976).

Comparisons: The three species of *Octodon* currently recognized can be distinguished from *O. pacificus* n. sp. as follows:

Octodon degus, type species of the genus, is smaller and has a stouter body; it has a shorter tail with a thick terminal brush, a coarse, agouti-coloured fur, a lighter venter and white ear tufts. In five specimens examined the pollex bears a small but clearly pointed claw, which contrasts to the reduced nail of the new species. The statement of Osgood (1943) that the species of the genus *Octodon* bear a nail on the pollex is not always correct. Bennett (1832), when diagnosing the genus *Octodon* and his new species *cumingii* (a synonym of *degus*), correctly stated that "the thumb of the fore feet has a short obtuse claw", not a nail. Nevertheless, Osgood's statement is equally found in standard references such as Woods and Boraker (1975). It may be possible that the character is variable but this has to be checked in a larger series. The observed differences between *O. degus* (claw) and *O. pacificus* n. sp. (nail), however, are very clear and rather suggest the existence of a good diagnostic character. The skull of *O. degus* is smaller and the position of the zygomatic arch is lower (Fig. 2). This species has the simplest molars of the genus (Fig. 6): upper and lower molariform teeth are fairly symmetrical and approach an 8-shape more than any other *Octodon.*

Octodon lunatus is similar to *O. degus* externally and cranially, although Osgood (1943) claimed that his new species was indistinguishable from *O. bridgesii.* The specimen at hand matches perfectly the description of Osgood, particularly with respect to the lunariform third upper molar (Fig. 6). Externally, the specimen differs from *degus* by a somewhat softer and longer pelage although the agouti colour is very similar. The underside of the skin, however, is paler and washed with cream-white. Yellow ear tufts are present. The dorsal surfaces of hands and feet are white. The pollex of the manus bears a nail, not a claw. The tail is long with a prominent terminal brush, dorsally dark brown, ventrally white on the first half and blackish-brown on the terminal part. Long whitish guard hairs are present mainly on the posterior part of the fur. The skull is similar to *O. degus* and *O. bridgesii,* but the M3 is diagnostic (Fig. 6).

Octodon bridgesii is similar to *O. pacificus* n. sp. in the softer texture of the fur, and in its trend towards asymmetry of the teeth (Figs. 5, 6). In addition, the pelage is more uniform and lacks white or yellow ear tufts. The colour of the body hairs is a mixture of brown and yellow, not orange. The tail is shorter (75 % of head and body length) but is similar to *pacificus* n. sp. in not having such a prominent terminal tuft (Waterhouse 1844; Mann 1958) as in *O. degus* and *O. lunatus.* Averages for *Octodon bridgesii* are smaller for all measurements (Tab. 2). Clear-cut differences to *O. pacificus* n. sp. exist in the size and shape of the skull, the shape and position of the zygomatic arch (Fig. 3), and in the size and form of the molariform teeth (Fig. 6), particularly in the upper and lower third molars.

History of discovery: The discovery of this new rodent has been a matter of enthusiastic research effort and personal tragedy. One person involved is Dr. Francisco Behn (11. 6. 1910–28. 5. 1976), formerly a Professor of Anatomy and Pathology at the University of Concepción, Chile, and a free-time ornithologist. Although occupied by his profession he also spent his free time with the study of birds and such contributed to the ornithology of Chile (Behn and Millie 1957). Together with his wife Erika Behn he brought together an important collection of birds from northern Chile to Antarctica. For many years he corresponded with Dr. Günther Niethammer (28. 9. 1908–14. 1. 1974), at that time curator of birds at the Museum Alexander Koenig, Bonn, whom he knew personally from a visit to Bonn in 1954, as evidenced by documents in the archives of the Bonn Museum. In 1959 Dr. Behn and his family made an expedition to Isla Mocha where they camped for two weeks. On the first of September, 1959, he wrote to G. Niethammer [translated from German]: "All of January I visited an ornithologically extremely interesting island, which is situated some kilometres south of Concepción off the mainland: the so-called Isla

Mocha. It has been studied only once before in more detail by a bird watcher, since access is only possible by aircraft which has to land on the beach or on one of the meadows."

In his letter BEHN enthusiastically continued to talk about his observations on the nesting habits of a seabird, *Puffinus creatopus,* which he planned to write up and publish as soon as his busy professional life would allow. For unknown reasons he never did so and all his experience was lost with his death in 1976. It remained also unknown that on his expedition to Isla Mocha he had collected a small number of mammals which he sent to G. NIETHAMMER's then 22 year-old son, JOCHEN NIETHAMMER, who later became Professor of Zoology at Bonn University. The specimens remained unstudied for more than thirty years in his private collection and came to light only recently when it was transferred to and curated at the Museum Alexander Koenig, a final consequence of his tragic car accident which happened on an excursion with students in July 1991. Severe injuries terminated the career of this well-known mammalogist, main editor of the "Handbook of European Mammals" and author of numerous papers on Palaearctic and African mammals, but also the discoverer of the extinct giant rat of the Galapagos Islands (NIETHAMMER 1964).

Etymology: The species is currently known only from a small island in the Pacific Ocean, hence its specific epithet.

Other mammals: Very little is known on the remaining mammal fauna of Isla Mocha. PHILIPPI (1900) described a new mouse as *Mus mochae,* which OSGOOD (1943) assigned to *Akodon olivaceus* (Waterhouse, 1837). OSGOOD (1943) also reported on three other rodent species obtained by D. S. BULLOCK in 1932 on this island. Apart from the new *Octodon* and samples of *Akodon longipilis castaneus* Osgood, 1943 (ZFMK 92.387–389), and *Akodon olivaceus mochae* (Philippi, 1900) (ZFMK 92.390–393), the small collection obtained by F. BEHN in 1959 contains a specimen of *Rattus rattus* Linnaeus, 1758 (ZFMK 92.394), a species which has not been reported from this island before. Table 4 summarises

Table 4. **Mammals recorded from Isla Mocha, based on PHILIPPI (1990), OSGOOD (1943), and the present report**

	Collectors		
	PHILIPPI (1900)	BULLOCK (1932)	BEHN (1959)
Octodon pacificus n. sp.			x
Akodon longipilis		x	x
Akodon olivaceus	x	x	x
Geoxus valdivianus		x	
Oryzomys longicaudatus		x	
Rattus rattus			x

the small mammal species so far known from Isla Mocha. The cricetine rodents listed are characteristic for the temperate Valdivian rain forest on the neighbouring mainland (MESERVE et al. 1982). However, the material from Isla Mocha stored at the American Museum, the British Museum, and the Bonn Museum deserves careful study of its own. Some subspecies named for populations of Isla Mocha may in fact represent full species. This seems probable for *Akodon longipilis castaneus,* the skull of which differs markedly from what REIG (1987) figured as representing the typical mainland population of *A. longipilis.*

Relationships within the genus *Octodon*

Looking at morphological characters, the four extant species of *Octodon* fall into two groups. One includes *O. bridgesii* and the new species, the other *O. degus* and *O. lunatus.* The first two species share the following characters: uniform colouration, soft pelage, short ears, long but inconspicuously tufted tail, asymmetrical teeth with a long reentrant fold. Photographs of live *O. bridgesii* and *O. degus* in Reise and Venegas S. (1987) neatly illustrate the external differences. *O. degus* and *O. lunatus* share the more vivid colouration, hairs of agouti-type, light eye marks, larger and tufted ears, pronounced black tail tufts, less asymmetrical teeth, and highly reduced third molars. The author regards most of the characters of the first group as primitive and those of the second group as derived for the genus.

The supposed polarities are based on an outgroup comparison with fossil Octodontidae (Wood 1949; Pascual 1967; Patterson and Wood 1982; Reig and Quintana 1991), Ctenomyidae (Pascual et al. 1965; Reig 1970; Verzi et al. 1991) and Echimyidae (Patterson and Pascual 1968; Lavocat 1976), particularly with the Oligocene *Platypittamys brachyodon* Wood, 1949, which is often taken as an ancestor model for the living Octodontidae. This assumption is justified because fossils of *Platypittamys* share a characteristic enamel structure with the extant Octodontoidea (Martin 1992), but not with other Caviomorpha. It should, however, be noted that Reig and Quintana (1991) presented a different view of molar evolution in octodontids which will be discussed below.

An ingroup comparison reveals that *Octodon pacificus* n. sp. assembles more plesiomorphic characters than the other three species. The high position of the zygomatic process of the squamosal is only found in *O. pacificus* n. sp. (Fig. 2); it is shared with *Platypittamys* (Wood 1949). *Platypittamys* and some other fossil octodontids have strongly asymmetrical and homodont molars (Wood 1949). Within genus *Octodon, O. pacificus* n. sp. approaches these conditions more than the other species (Figs. 6, 8). A reduction of the third molars, as in *O. degus* and *O. lunatus,* is certainly a derived feature and may be a general evolutionary trend in octodontoid rodents.

In conclusion, *Octodon pacificus* n. sp. may be regarded as the most primitive species of the genus. Geographically isolated and in the absence of similar-sized competitors the species may have lived on Isla Mocha since the Miocene, the geological age of the island (Tavera and Veyl 1958). Some morphological changes, however, must have occurred, as the large infraorbital foramen and the backward position of the superior zygomatic root (Fig. 3) are derived characters. *O. pacificus* n. sp. and *O. bridgesii* most probably had a common ancestor; both share a similar morphology and possibly similar ecological requirements. They have the southernmost distributions of the genus (Fig. 7) and seem to be more restricted to forest (Greer 1968; Meserve et al. 1982) than *O. degus* and *O. lunatus* which are adapted to life in semiarid shrublands (Woods and Boraker 1975; Contreras et al. 1987; Meserve and Le Boulengé 1987; Bozinovic 1992).

How does this interpretation fit with the available chromosomal data? *O. degus* and *O. bridgesii* have 58 chromosomes (Gallardo 1992), while *Octodon lunatus* has 78 (Spotorno et al. 1988) (Tab. 5). Gallardo (1992) discussed in detail the polarities of the karyotypes concluding that 58 represents the plesiomorphic condition and the higher number of 78 a derived condition. This view, which is in contradiction to Spotorno et al. (1988), is in full congruence with the morphological conclusions made above.

Comparisons with other Octodontidae

It is a matter of curiousity that the type genus of the family, *Octodon,* does not show the character for which it was named (Fig. 8). 8-shaped teeth are found in *Aconaemys* (Mann

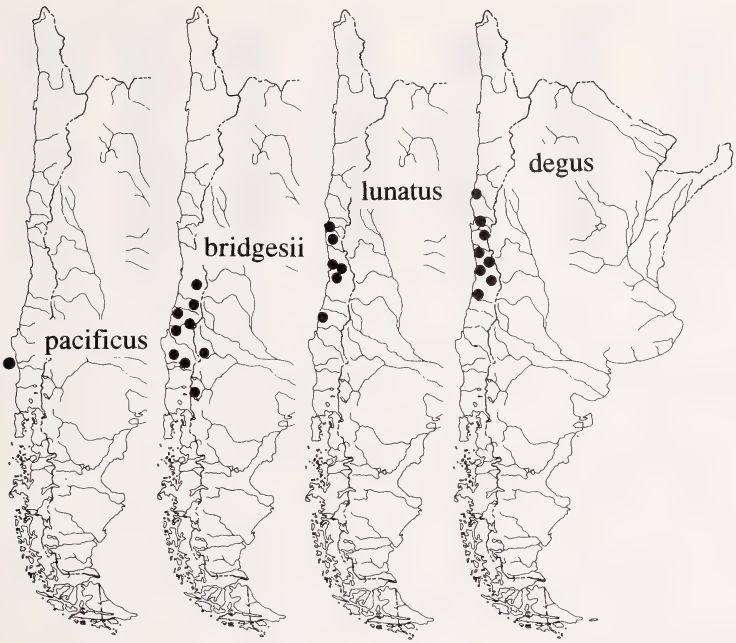

Fig. 7. Maps of Chile and Argentina with the approximate distributions of the four species of *Octodon* indicated; in part adopted from Redford and Eisenberg (1992), modified

1958; Glanz and Quintana 1991), and *Spalacopus* (Reig 1970), while *Octodon* (Figs. 6, 8) and *Octodontomys* (Glanz and Anderson 1990) have asymmetrical teeth; the latter genus has no reentrant folds at all. If we look again at *Platypittamys* (Fig. 8), we would have to take *Octodon* as the most primitive genus of Octodontidae, with *Octodontomys* perhaps as an offshoot of *Octodon,* and *Aconaemys, Octomys, Tympanoctomys,* and *Spalacopus* as members of a more derived clade. This grouping coincides largely with Thomas (1920), who divided the then known genera in a group with "crescentic" and another with "8-shaped teeth". Reig and Quintana (1991) argued for the contrary. They did not mention *Platypittamys* but stated that 8-shaped molars, as in *Aconaemys,* are primitive and asymmetrical ones, as in *Octodon,* are derived, a view obviously taken from the Miocene *Pseudoplataeomys elongatus* which has perfectly 8-shaped molars (Reig and Quintana 1991). They also described a new genus, *Abalosia,* from the Pleistocene of Argentina, which in their interpretation may have been the ancestor of genus *Octodon.* While the present author can concur that *Pseudoplataeomys* may have been ancestral to the group of octodontids with 8-shaped molars *(Aconaemys, Octomys, Tympanoctomys, Spalacopus),* it does not follow that *Octodon* is derived from the Pleistocene *Abalosia.* This genus has very simple molars resembling *Octodontomys* (Fig. 8) but it also has very long upper third molars which are quite unusual for the group. Also the skull of *Abalosia,* as figured by Reig and Quintana (1991), is not similar to *Octodon* but instead recalls the skull of *Aconaemys* with its short nasals, broad interorbital region, parallel molar rows, and stout mandible. The phylogenetic position of Abalosia should thus be regarded as uncertain and its postulated relation to *Octodon* cannot be accepted. If we include the Oligocene *Platypittamys* in this comparison then again *Octodon* would group next to it (Fig. 8). The Pliocene *Chasicomys octodontiforme* Pascual, 1967 shows a somewhat intermediate morphology of the upper molars (Pascual 1967) and may be taken as support for the supposed direction of molar evolution. It can be supposed that different groups of

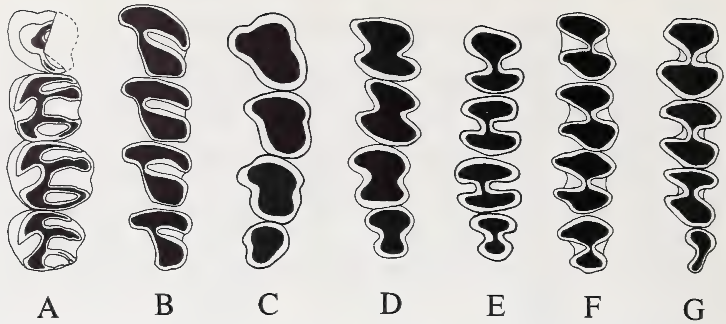

Fig. 8. Right upper molars of octodontid rodents. A: *Platypittamys brachyodon* (copied from Wood 1949, slightly simplified); B: *Octodon pacificus* n. sp. (paratype); C: *Octodontomys gliroides* (copied from Reig and Quintana 1991, reversed); D: *Spalacopus cyaneus* (ZFMK 92.310); E: *Tympanoctomys barrerae* (copied from Reig and Quintana 1991, reversed); F: *Aconaemys fuscus* (ZFMK 88.59); G: *Octomys mimax* (copied from Ellerman 1940, modified). Not to scale, tooth rows brought to approximately the same length for the purpose of comparison

octodontids already diverged in the Miocene, and that their phylogeny is at present obscured by an incomplete fossil record. Verzi et al. (1991) also concluded from their work on fossil Octodontoidea that octodontine and ctenomyine rodents radiated contemporaneously in the Miocene.

If we neglect the molars and look only at the skull, then *Tympanoctomys* (Landry 1957; de Santis 1991) would be the candidate for the most primitive genus because of its small infraorbital foramen and the extremely anterior position of the superior zygomatic root, which is shared by *Platypittamys* but not by any of the other five genera. On the other hand, *Tympanoctomys* and *Octomys* (Thomas 1920; Walker et al. 1964) both have hypertrophied auditory bullae, certainly derived structures related to their gerbil-like habitus.

The chromosome complements, which surprisingly are known for all species except *Octodon pacificus* n. sp., present a slightly different picture (Tab. 5). *Aconaemys, Octomys, Spalacopus,* and *Octodon* have very similar karyotypes, whilst *Octodontomys* has a lower (38) and *Tympanoctomys* a much higher (102) chromosome number. The latter two genera may be taken as derived in this character.

Table 5. **Chromosome numbers of the species of Octodontidae; adopted from Gallardo (1992), Gallardo and Reise (1992), and references cited therein**

Species	2N	FN
Aconaemys fuscus	56	108
Aconaemys porteri	58	112
Aconaemys sagei	54	104
Octomys mimax	56	108
Spalacopus cyaneus	58	112
Octodon degus	58	112
Octodon bridgesii	58	112
Octodon lunatus	78	114
Octodontomys gliroides	38	64
Tympanoctomys barrerae	102	198

None of the different data sets provides a convincing solution of the phylogenetic relations between the six extant genera of Octodontidae, nor does the work based on blood protein similarities of only three genera (Woods 1982). At present it seems impossible to solve the phylogenetic relationships within the Octodontidae with the given information. One reason may be that the six extant genera represent only a small portion of the past diversity, a view held also by Gallardo (1992) and suggested by the fossils which are already known (Mones 1986; Reig and Quintana 1991) although many more fossils may be expected. Nevertheless, study of the fossil record together with the extant species allows the formulation of hypotheses on

evolutionary trends which could be tested in the future against more complete data sets based on other character complexes.

A note on island rodents and conservation

Since Osgood's comprehensive work (1943), the mammal fauna of Chile is regarded as one of the best-studied in South America (Patterson and Feigl 1987). The latter authors predicted that "further additions to the faunal list are apt to be those species with highly restricted geographic ranges, especially those in remote areas". This is perfectly true in the case of Isla Mocha, and counts also for two other rodents discovered on islands in southern Chile: *Akodon markhami* (Pine 1973) and *Akodon hershkovitzi* (Patterson et al. 1984). While those rodents were collected rather recently, the collection of the Pacific degu dates already from 1959. No attempts have been made since to check the actual status of the new species. It is not known whether it still forages in the meadows or forest of Mocha Island, nor, in the positive case, how large the population may be. What seems certain is that the natural range of the species covers only a few square kilometres and for this reason alone it must be regarded as vulnerable. Soft fur, orange-brown colour and the long tail suggest that this degu lives in the forest, thickets or swamps, which are restricted habitats on the island. In a report on the endangered mammals of Chile Miller et al. (1983) classified one of the mainland species, *Octodon bridgesii,* as vulnerable. They stated that the range of the species had been much reduced, presumably by increased cultivation of its valley habitat. If this is true for a rather widespread species, then such threats may apply even more to a small island population. The sample of Francisco Behn also shows (Tab. 4) that black rats were already present on Isla Mocha in 1959. Numerous examples show how fast endemic mammal faunas on islands are destroyed by human occupation, just to mention the Galapagos (Steadman and Ray 1982), the West Indies (Morgan and Woods 1986), or the Canary Islands (Boye et al. 1992). In the case of Mocha Island, a considerate field survey is suggested to test whether the Pacific degu still exists. Chilean mammalogists should feel encouraged to study this aspect and propose conservation measures, if necessary.

Acknowledgements

I owe gratitude to Mrs. Erika Behn, who sent me valuable information on Isla Mocha and even a short film taken during the 1959 expedition in which she participated. Dr. F. Dieterlen, Dr. G. Storch and Prof. Dr. W. von Koenigswald provided important specimens from their collections for study. Dr. K. Busse shared his knowledge of Chile and procured rare literature, and Mrs. H. von Issendorff, Dr. G. Peters and Dr. G. Storch critically read and improved the manuscript. The photographs are the work of Mr. H. Meurer. I am grateful to all of them.

Zusammenfassung

Nagetiere auf Inseln: eine neue Octodon-Art von der Isla Mocha, Chile (Mammalia: Octodontidae)

Auf der 31 km vor der chilenischen Küste gelegenen Insel Mocha lebt ein bisher unbekannter Degu, der unter dem Namen *Octodon pacificus* n. sp. beschrieben wird. Es handelt sich um eine große, weichhaarige und langschwänzige Art von einheitlich braun-orangener Färbung, der helle Überaugenstreifen oder Ohrbüschel fehlen. Weiterhin bemerkenswert sind die homodonte Backenbezahnung und die asymmetrische Form der molariformen Zähne, deren linguale Schmelzfalten vollständig mit Zement ausgefüllt sind. Im Vergleich zu fossilen Octodontidae erweisen sich die meisten Merkmale der neuen Art als plesiomorph; nächstverwandt dürfte *Octodon bridgesii* sein, während *O. degus* und *O. lunatus* einer anderen abgeleiteten Gruppe zugerechnet werden. Beziehungen der 6 rezenten Gattungen der Familie untereinander und zu fossilen Vertretern werden diskutiert. Der neue Pazifik-Degu ist offenbar eine Reliktart, die auf der kleinen Insel Mocha überlebt hat. Das vorhandene Belegmaterial wurde bereits 1959 von dem chilenischen Arzt Francisco Behn gesammelt. Der gegenwärtige Status der Art ist nicht bekannt.

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Author's address: Dr. RAINER HUTTERER, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 162, D-53113 Bonn 1, Germany

Z. Säugetierkunde 59 (1994) 42–51

ISSN 0044-3468

Allozyme divergence and systematics of Common mole-rats (*Cryptomys*, Bathyergidae, Rodentia) from Zambia

By Maria G. Filippucci, H. Burda, E. Nevo, and J. Kocka

Department of Biology, University of Roma "Tor Vergata", Roma, Italy; Department of Morphology, Johann-Wolfgang-Goethe-University, Frankfurt am Main, Federal Republic Germany; Institute of Evolution, University of Haifa, Haifa, Israel, and Surgery Department, University Teaching Hospital, Lusaka, Zambia

Receipt of Ms. 3. 11. 1992
Acceptance of Ms. 28. 12. 1992

Abstract

Studied allozymic diversity encoded by 34 gene loci in African common mole-rats, *Cryptomys* sp., comprising two populations from Zambia and re-analyzed allozymic diversity encoded by 25 gene loci in *Cryptomys damarensis, C. hottentotus,* and *C. natalensis* from South Africa. This is the first genetic study of *Cryptomys* populations originating from outside the South African Subregion. The dichotomy between *C. damarensis* on the one hand and *C. hottentotus* and *C. natalensis* on the other hand revealed by previous studies was reconfirmed. Both Zambian populations are specifically distinct from each other and both are distant from all the South African species. Zambian *Cryptomys* are much closer to *C. damarensis* than to both other species. Interpretation of results of the allozymic study is corroborated by data on other biological aspects. We show that currently used morphological criteria for classification of *Cryptomys* are apparently wrong and that the genus *Cryptomys* requires urgently a modern large-scale revision based on allozymes, karyotypes and phenotypic variations.

Introduction

"As a rule, systematic difficulties and doubts arise largely from a paucity of specimens; but *Cryptomys* is a genus which by comparison is already fairly abundantly represented in museums, and every addition so far from making the situation clearer only seems to add to the confusion" (Rosevear 1969, p. 561).

The family Bathyergidae includes subterranean rodents endemic to Africa. It is agreed that the systematic study of this family may elucidate many aspects of evolutionary biology like historical biogeography of Africa, the evolution of eusociality, and the classification and patterns of morphological evolution in rodents (Honeycutt et al. 1991). The family is currently placed into the suborder Hystricognathi, yet even almost fifty years after Simpson's (1945) statement that "Everyone agrees that (bathyergids) are extraordinarily isolated among rodents", a sister-group relationship between the Bathyergidae and any single lineage within the Hystricognathi could not be established (Honeycutt et al. 1991). The family is divided into five genera, the intergeneric relationships being far from clear (see Honeycutt et al. 1991 for the most recent review).

Particularly interesting is the genus *Cryptomys* which, from the standpoint of sociobiology, is considered by some authors as an intermediate link between solitary bathyergids and eusocial naked mole-rats (*Heterocephalus*) (e. g. Jarvis and Bennett 1991; Lovegrove 1991). Unlike other bathyergid genera, *Cryptomys* as a genus is rather eurybiomic (sensu Vrba 1992), occurring from semi-arid to mesic habitats in different soil types over a wide geographical range from Ghana to the Cape (Rosevear 1969). Although it is not a problem to recognize *Cryptomys* as *Cryptomys*, extreme variation in many morphological traits makes taxonomic treatment of this genus very difficult. Thus for instance, 44 and 49 species of *Cryptomys* have been named by Allen (1939) and Ellerman (1940), respec-

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tively. This number has been reduced to three species by later authors (cf. NOWAK and PARADISO 1983). Most recently, seven species have been recognized by HONEYCUTT et al. (1991). Different traits like the average size, pelage colouration, white head spots and other markings, shape and size of the infraorbital foramen as well as some other cranial characters have been used for determination and classification by different authors. However, many authors reported significant polymorphism in body size and pelage colouration (which is age and social-dependent in Zambian *Cryptomys*, BURDA 1989, 1990), and in white markings even within a single colony. These traits thus cannot be used for species diagnosis if only a small sample is available. Consequently, ROSEVEAR (1969) and ALLEN (1978) suggested that, in addition to morphological characters, cytology and serology should be brought into account before any reliable taxonomic opinion can be expressed.

Four recent cytologic and genetic studies gave stimuli to revise phylogenetic relationships among bathyergids: NEVO et al. (1986) analyzed karyotype differentiation, NEVO et al. (1987) allozyme differentiation, HONEYCUTT et al. (1987) mitochondrial DNA restriction-fragment variation, and HONEYCUTT et al. (1991) mitochondrial nucleotide-sequence variation. With respect to *Cryptomys*, it was demonstrated that two or perhaps even three distinct species, possibly even falling into two genera, can be recognized among the South African forms: *C. damarensis* on the one hand, and *C. (hottentotus) hottentotus* and *C. (hottentotus) natalensis* on the other hand. However, the use of these data for reconstruction of the biogeographic history, evolution of sociality, and intrageneric relationships of *Cryptomys* is limited by the fact that only South African populations were studied, while the genus is much more widely distributed.

We analyzed allozyme diversity in two populations of common (small) *Cryptomys* from Zambia. The present study thus becomes the first genetic investigation of *Cryptomys* from outside the South African Subregion.

Material and methods

Electrophoretic analysis was carried out on 14 specimens of African common mole-rats, *Cryptomys* sp. (Bathyergidae, Rodentia), representing two populations from Zambia, characterized by two different diploid chromosomal numbers (BURDA et al. 1992). The karyotype 2 n = 68 originated from Lusaka (locality Chainda in eastern suburbs of Lusaka, vicinity of the University Campus), the animals of the karyotype 2 n = 58 were captured in Itezhi-Tezhi (locality Hot Springs; about 200 km SWW of Lusaka). These two populations were also compared with samples of *C. hottentotus, C. natalensis* and *C. damarensis* from South Africa, involved also in previous analyses by NEVO et al. (1987).

Tissues of each specimen were preserved in the laboratory at −80 °C until processed. Homogenates for electrophoresis were obtained from portions of muscle and kidney tissues crushed in distilled water. Genic variation of structural genes encoding for enzymatic and non-enzymatic proteins was assessed using standard horizontal starch-gel electrophoresis. All gels were prepared using an 11 % suspension of Connaught hydrolyzed starch.

Homogenates obtained from muscle were processed for the following enzymatic proteins: α-Glycerophosphate dehydrogenase (E.C. 1.1.1.8; α-Gpdh), Lactate dehydrogenase (E.C. 1.1.1.27; Ldh-1 and Ldh-2), Malate dehydrogenase (E.C. 1.1.1.37; Mdh-1 and Mdh-2), Malic enzyme (E.C. 1.1.1.40; Me-1 and Me-2), Isocitrate dehydrogenase (E.C. 1.1.1.42; Idh-1 and Idh-2), 6-Phosphogluconate dehydrogenase (E.C. 1.1.1.44; 6-Pgdh), Glucose-6-phosphate dehydrogenase (E.C. 1.1.1.49; G-6-pdh), Indophenol oxidase (E.C. 1.15.1.1; Ipo-1 and Ipo-2), Nucleoside phosphorilase (E.C. 2.4.2.1; Np), Glutamate-oxalacetate transaminase (E.C. 2.6.2.1; Got-1 and Got-2), Hexokinase (E.C. 2.7.1.1; Hk-1), Creatine kinase (E.C. 2.7.3.2; Ck), Adenylate kinase (E.C. 2.7.4.3; Adk), Phosphoglucomutase (E.C. 2.5.7.1; Pgm-1 and Pgm-2), Esterases (E.C. 3.1.1.1; Est-1, Est-2 and Est-3), Acid phosphatase (E.C. 3.1.3.2; Acph), Aminopeptidase (E.C. 3.4.1.1; Ap-1 and Ap-2), Adenosine deaminase (E.C. 3.5.4.4; Ada), Fumarase (E.C. 4.2.1.2; Fum), Mannose phosphate isomerase (E.C. 5.3.1.8; Mpi), and Glucose phosphate isomerase (E.C. 5.3.1.9; Gpi). Homogenates obtained from kidney were processed for the following enzymatic proteins: Alcohol dehydrogenase (E.C. 1.1.1.1; Adh), Sorbitol dehydrogenase (E.C. 1.1.1.14; Sdh), and Xanthine dehydrogenase (E.C. 1.2.3.2.; Xdh).

The employed procedures were described earlier by Nevo et al. (1987) and Filippucci et al. (1988). Isozymes were numbered in order of decreasing mobility from the most anodal one. Allozymes were designated numerically according to their mobility, relative to the most common allele (= 100) (< 100 = slower mobility; > 100 = faster mobility) in *C. (h.) hottentotus* from South Africa.

Allozymic data were analyzed as genotype frequencies with the BIOSYS-1 program of Swofford and Selander (1981). Intrapopulational genetic variation was estimated by the following genetic indices: the mean heterozygosity per locus (observed, Ho, and expected, He), the proportion of polymorphic loci in the population (P 1 %: a locus is considered polymorphic if the frequency of the common allele is not greater than 0.99), and the average number of alleles per locus (A). The amount of genetic divergence between populations was estimated with the indices of standard genetic identity (I) and distance (D) proposed by Nei (1972).

The two populations from Zambia were analyzed for 34 loci. The comparison with the other South African species was carried out on 25 shared loci; the following loci were excluded from this analysis: Shd, Me-2, Ipo-1, Ipo-2, Ck, Adk, Ap-2, Fum, and Est-3.

A dengrogram of the genetic relationships among populations was obtained using the unweighted pair group cluster analysis UPGMA (Sokal and Sneath 1963).

Results

Biological divergence

Some of the relevant intrinsic (morphological, reproductive, sociobiological) as well as extrinsic (ecological) characteristics of Zambian (and South African) *Cryptomys* and their habitats are provided and compared in table 1. Representatives of both populations (Lusaka and Itezhi-Tezhi) possessed eliptical infraorbital foramina (6 skulls of 2n = 68, 3 skulls of 2n = 58 were examined). Two mixed pairs consisting of females of the karyotype 2 n = 68 and males of the 2n = 58 karyotype were kept for seven months. The animals mated normally and regular copulations (observed at least three times a week) were elicited by constant re-pairing of animals (cf. Burda 1989). Both females conceived at least once but resorbed or aborted the embryos within three to four weeks. Even after seven months there was no offspring to any of both females. Subsequent pairing with conspecifics of the same karyotype resulted within few weeks in conception, successfull pregnancy and delivery, and thus confirmed the normal fertility of the involved animals. Further "hybridization" experiments are in progress. They are negative thus far.

Table 1. **Some characteristics of *Cryptomys* and their habitats**

Based on Jarvis and Bennett (1991) and further studies of Bennett and Jarvis cited therein for South African taxa; and on Burda (1989, 1990) for Zambian mole-rats. The given weights refer to mean weights of grown up breeding animals

Species	2n	Weight (g) f	Weight (g) m	Gestation (days)	Eyes open (days)	Colony size	Rainfall (mm/year)
Lusaka	68	75	110	98	24	<25	840
Itezhi-Tezhi	58	75	110	?(>70)	?	?(>12)	>800
C. damarensis	74, 78	155	200	85	18	<25	200–600
C. hottentotus	54	65	75	63	13	<14	200–500
C. natalensis	54	90	105	?	?	?(2–3)	400–600

Pattern of variation

Twenty-three of the thirty-four loci analyzed were monomorphic and fixed for the same allele in the two populations from Zambia: Adh, Sdh, Ldh-1, Ldh-2, Mdh-2, Me-1, Me-2, Idh-1, Idh-2, Ipo-1, Ipo-2, Np, Got-2, Ck, Adk, Pgm-1, Pgm-2, Ap-1, Ap-2, Ada, Fum,

Table 2. **Allelic frequencies observed at the polymorphic and/or discriminant loci for the analyzed populations of the genus *Cryptomys***

Number of examined specimens in parentheses

Loci	Alleles	Lusaka (12)	Itezhi-Tezhi (2)	*C. hott.* (4)	*C. nat.* (4)	*C. dam.* (1)
Adh-1	100	1.00	1.00	1.00	1.00	–
	110	–	–	–	–	1.00
αGpdh	100	–	–	0.87	1.00	–
	103	–	–	–	–	1.00
	104	–	–	0.13	–	–
	106	0.92	0.25	–	–	–
	110	0.08	0.75	–	–	–
Ldh-1	100	1.00	1.00	0.75	1.00	1.00
	105	–	–	0.25	–	–
Mdh-1	100	1.00	0.50	1.00	1.00	1.00
	105	–	0.50	–	–	–
Mdh-2	95	1.00	1.00	–	–	1.00
	100	–	–	1.00	1.00	–
Me-1	98	–	–	–	0.25	–
	100	–	–	0.92	0.75	–
	105	–	–	0.08	–	–
	110	1.00	1.00	–	–	1.00
6Pgdh	90	–	–	–	1.00	–
	95	–	0.25	–	–	–
	100	–	0.75	1.00	–	–
	103	–	–	–	–	1.00
	105	1.00	–	–	–	–
G6pdh	95	0.79	1.00	0.10	0.33	1.00
	100	0.21	–	0.90	0.67	–
Xdh	100	0.85	1.00	1.00	1.00	1.00
	105	0.15	–	–	–	–
Np	100	1.00	1.00	0.83	0.75	0.50
	103	–	–	0.17	0.25	0.50
Got-1	90	0.75	–	–	–	–
	100	0.25	1.00	1.00	1.00	–
	105	–	–	–	–	1.00
Hk-1	100	0.96	1.00	1.00	1.00	1.00
	105	0.04	–	–	–	–
Pgm-2	100	–	–	1.00	1.00	1.00
	103	1.00	1.00	–	–	–
Ap-1	100	–	–	1.00	1.00	–
	108	1.00	1.00	–	–	1.00
Ada	96	–	–	0.08	–	–
	100	–	–	0.92	1.00	–
	105	1.00	1.00	–	–	1.00
Mpi	100	–	–	1.00	1.00	–
	110	1.00	1.00	–	–	1.00
Pgi	90	–	0.75	–	–	–
	96	0.12	–	–	–	–
	100	0.88	0.25	1.00	1.00	1.00

Table 2 (continued)

Loci	Alleles	Lusaka (12)	Itezhi-Tezhi (2)	*C. hott.* (4)	*C. nat.* (4)	*C. dam.* (1)
Acph	100	0.05	–	0.88	1.00	–
	105	0.95	–	0.12	–	1.00
	110	–	1.00	–	–	–
Est-1	100	–	–	0.90	0.88	–
	105	1.00	0.25	–	0.12	1.00
	108	–	0.75	0.10	–	–
Est-2	100	1.00	1.00	0.88	1.00	1.00
	105	–	–	0.12	–	–
Est-3	100	0.88	1.00			
	105	0.12	–			

Mpi, Est-2. The allele frequencies of the polymorphic and/or discriminant loci in the two populations from Zambia and in *C. hottentotus, C. natalensis* and *C. damarensis* from South Africa are given in table 2. For detailed allele frequencies in South African populations see NEVO et al. (1987).

The population from Lusaka (2n = 68) displayed polymorphism at the following loci: αGpdh, G6pdh, Got-1, Hk-1, Pgi, Acph, Xdh, and Est-3.

The population from Itezhi-Tezhi (2n = 58) was polymorphic at the following loci: αGpdh, Mdh-1, 6Pgdh, Pgi, and Est-1.

Genetic summary

The mean value of observed heterozygosity, based on 34 loci, for the populations from Zambia was Ho = 0.052 (Ho = 0.045 in Lusaka and Ho = 0.059 in Itezhi-Tezhi). The mean value of expected heterozygosity was He = 0.066 (He = 0.054 in Lusaka and He = 0.078 in Itezhi-Tezhi). The overall mean proportion of polymorphic loci (P 1 %) for the two populations was P 1 % = 0.191 (P 1 % = 0.253 in Lusaka and P 1 % = 0.147 in Itezhi-Tezhi). The overall mean number of alleles per locus was A = 1.19 (A = 1.24 in Lusaka and A = 1.15 in Itezhi-Tezhi).

Genetic differentiation

Two loci (6Pgdh and Acph) were found discriminant between Lusaka and Itezhi-Tezhi, displaying fixation of alternative alleles. Five loci (αGpdh, Mdh-1, Got-1, Pgi, Est-1) partially discriminated the two populations.

Genetic distance

The values of genetic identity and distance (NEI 1972) between Lusaka and Itezhi-Tezhi populations were I = 0.871 and D = 0.138 respectively.

The values of NEI's genetic identity and distance observed on 25 shared genetic loci between the three South African *Cryptomys* species and both Zambian populations are given in table 3. An UPGMA dendrogram summarizing the genetic relationships found between the populations studied is given in figure 2. In this comparison, the two populations from Zambia displayed a higher value of genetic distance (D = 0.196). The populations from Zambia displayed very high values of genetic distance in comparison with those from South Africa. The values of genetic distance ranged from 0.237 to 0.596. Both populations showed higher affinity with *C. damarensis* (D = 0.300, ranging from

Table 3. **Values of NEI's genetic identity (I; above the diagonal) and distance (D; below the diagonal) between populations of the genus *Cryptomys* from Zambia and South Africa, based on 25 loci**

Population	1 Lusaka	2 Itezhi	3 *C. hott.*	4 *C. nat.*	5 *C. dam.*
1 Lusaka	–	0.822	0.551	0.563	0.789
2 Itzehi-Tezhi	0.196	–	0.571	0.552	0.695
3 *C. hottentot.*	0.596	0.561	–	0.947	0.520
4 *C. natalensis*	0.574	0.594	0.055	–	0.539
5 *C. damarensis*	0.237	0.364	0.654	0.618	–

0.237 in comparison with Lusaka to 0.364 in comparison with Itezhi-Tezhi populations). Equivalent were instead the mean values observed comparing *Cryptomys* from Zambia with *C. hottentotus* (D = 0.578) and *C. natalensis* (D = 0.584).

Discussion

According to GORMAN and RENZI (1979), in populations with small sample size (Itezhi-Tezhi), the heterozygosity could change by less than 2.5 % as compared with a larger sample size. The high number of loci analyzed compensates for the small sample size of some populations. Values of heterozygosity and genetic distances are therefore reliable with a reasonable margin of precision (SARICH 1977; NEI 1978; GORMAN and RENZI 1979; SAGE et al. 1986).

The observed values of genetic variation correspond to the values already observed in South African species of *Cryptomys* by NEVO et al. (1987) and are within the range generally reported for other Rodentia and even that of subterranean rodents which usually display lower genetic variation than above-ground rodents (NEVO et al. 1990).

Our findings on relationships of South African *Cryptomys* corroborate results of previous studies by HONEYCUTT et al. (1987, 1991) and NEVO et al. (1987) in confirming the dichotomy between *C. damarensis* and *C. hottentotus*, the latter taxon splitting again into two distinct forms: *hottentotus* and *natalensis*.

We suggest that the analyzed Zambian populations comprise two good biological species which are related yet distinct from each other. The distinction is suggested not only by a high value of NEI's D (this study) but also by different karyotypes (BURDA et al. 1992), and (if not absolute then for sure relative) postmating reproductive barrier. Whether there is also a premating barrier in nature is not clear. The boundary between both species could not be determined thus far. Using NEI's (1975) criteria (based, however, on presumption of neutrality) (cf. also NEVO et al. 1987), the divergence time (= 5×10^6 D) between the two Zambian populations would be about 700 000 (based on 34 loci) to 1 million years (based on 25 loci).

Based on allozymic data, Zambian *Cryptomys* are clearly distinct from all South African taxa. This divergence is confirmed also by different karyotypes (NEVO et al. 1986; BURDA et al. 1992) and by (combination of) some biological aspects (e.g. regular age-dependent colour changing in both Zambian *Cryptomys* BURDA 1989, 1990, which is absent in *C. damarensis*, LOVEGROVE pers. comm., and in fact was never noticed in literature dealing with ontogenetic and social development in South African *Cryptomys* – cf. BENNETT et al. 1991 and literature cited therein).

Although the examined populations of Zambian *Cryptomys* for sure represent good species, distinct from each other and from the South African taxa, it would be preliminary to describe them formally as new species and to provide them with new specific names.

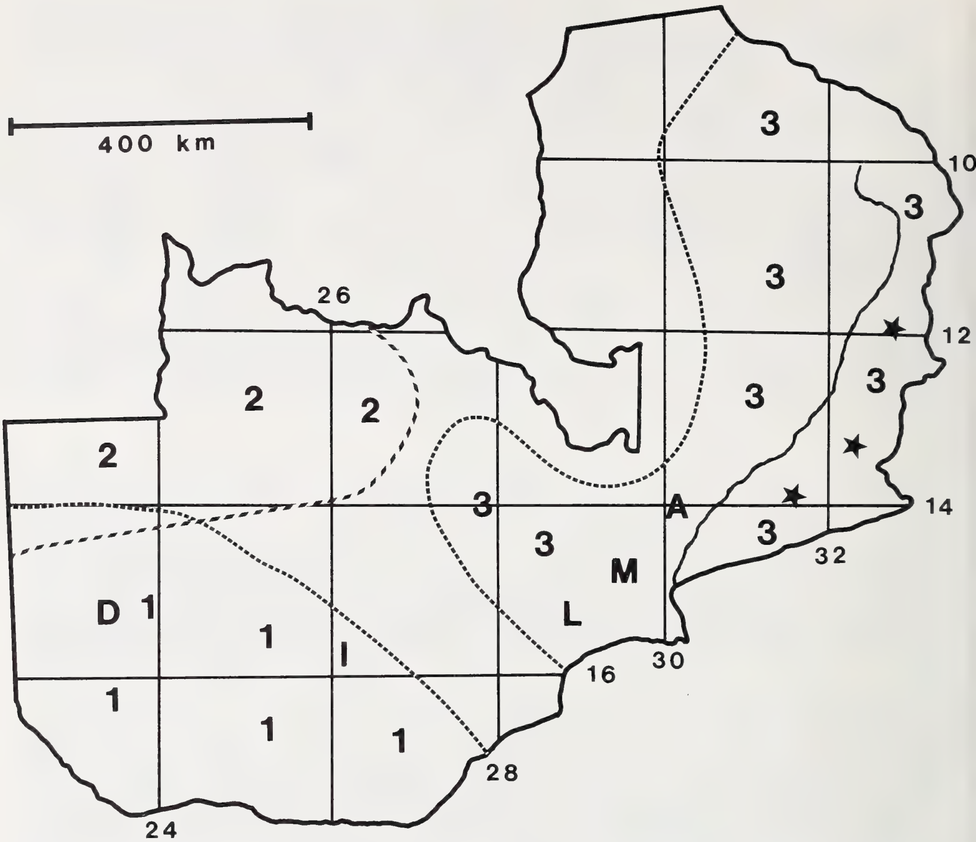

Fig. 1. Map of Zambia. Typical localities of *Cryptomys* taxa described from (what is now) Zambia (according to Allen 1939; Ansell 1978): A = *C. amatus,* D = *C. damarensis micklemi,* M = *C. molyneuxi.* Distribution of different species of common *Cryptomys* across Zambia (according to Honeycutt et al. 1991): 1 = *C. damarensis,* 2 = *C. bocagei,* 3 = *C. hottentotus* (ssp. *amatus*). Note, however, that according to Ansell (1978), no *Cryptomys* occur east of the Luangwa river (asterisk). Localities of *Cryptomys* described in this paper: I = Itezhi Tezhi (2n = 58), L = Lusaka (2n =68)

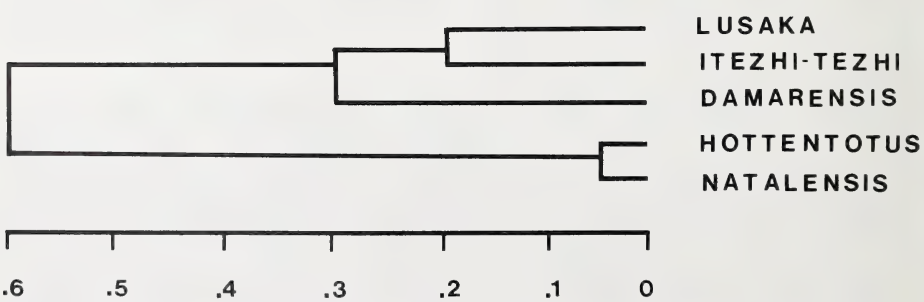

Fig. 2. UPGMA dendrogram summarizing the genetic relationship among populations of the genus *Cryptomys* from Zambia and South Africa, based on 25 loci. The cophenetic coefficient is 0.983

Our restraint is based on the fact that only from (what is now) Zambia, three taxa of common (small) *Cryptomys* were described (cf. ALLEN 1939): *C. amatus, C. damarensis (micklemi)*, and *C. molyneuxi*. DE GRAAFF (1971), ANSELL (1974), KINGDON (1974), and SMITHERS (1983) considered all Zambian common *Cryptomys* to be only subspecies of a single species, *Cryptomys hottentotus: C. h. hottentotus, C. h. damarensis* (syn. *micklemi*), *C. h. whytei* (syn. *occlussus*), and *C. h. amatus* (syn. *molyneuxi*) (see also Fig. 1). According to HONEYCUTT et al. (1991), three species of common *Cryptomys: C. hottentotus, C. damarensis*, and *C. bocagei* should occur in Zambia. The Lusaka population should belong to *C. hottentotus amatus*, while the mole-rats from Itezhi-Tezhi should represent *C. damarensis* (cf. Fig. 1). As stated above this was not the case. In order to avoid further nomenclatoric confusion, typical localities must be revisited and topotypical populations must be reexamined by further methods.

In this study we omit giant mole-rats (*Cryptomys mechowi/mellandi*) from Zambia which are for sure distinct from all other *Cryptomys* species (cf. also BURDA and KAWALIKA 1992). The animals which we called *C. hottentotus* in our previous studies belonged to the Lusaka population (2n = 68).

The systematical classification of all *Cryptomys* outside the South African Subregion was based on gross morphological traits only. HONEYCUTT et al. (1991) divided the seven recognized species into two groups according to the size and shape of the infraorbital foramen. According to the authors, small circular foramina can be found in the central and western African species (including *C. damarensis*) while eliptical foramina are typical of the "*hottentotus*" group inhabiting southern and eastern Africa (incl. Zambia).

In fact, representatives of both populations (Lusaka and Itezhi-Tezhi) possessed eliptical infraorbital foramina. However, ROSEVEAR (1969) (and previous authors quoted by him) and ANSELL (1978) reported significant variability in this trait and questioned its usefulness for systematic diagnosis and classification.

In contrast to the classification based on the cranial traits, our genetic findings show higher affinity of Zambian *Cryptomys* to *C. damarensis* rather than to *C. hottentotus*. This relatedness is corroborated also by reproductive (slower pre- and postnatal development) and sociobiological characters (larger families irrespective of diverse climatic and vegetational conditions), and by a more pronounced sexual dimorphism, which are similar in *C. damarensis* and Zambian *Cryptomys* but different from those in *C. hottentotus* (cf. Tab. 1). Apparently, the shape of the infraorbital foramen changed independently and parallelly in diverse lineages. Being most probably neither adaptive nor strictly conservative, this trait thus cannot be employed to elucidate sister relationships in *Cryptomys*.

Even only 200 km apart from each other, in comparable habitas, two distinct *Cryptomys* species were found. Analogously, in Israel across 200 km (however, in different climatic regions), four chromosomal species (considered good biological species) of *Spalax ehrenbergi* occur (e.g. NEVO 1991). We may expect similar speciation in *Cryptomys* range. A large-scale analysis employing karyotypes, allozymes plus other inputs (morphological, physiological, ecological, behavioural, reproductive, natural hybridization etc.) of the genus *Cryptomys* over a broad range of its distribution is needed to provide a definite answer to many interesting questions associated with historical zoogeography, adaptive radiation, and evolution of sociality of *Cryptomys* in particular (and bathyergids and subterranean mammals in general).

Acknowledgements

We thank Mr. M. KAWALIKA, Mrs. E. KOCKA and Mr. S. KRUNIC for their assistance in the field. E. NEVO thanks to the Israel Discount Bank Chair of Evolutionary Biology and to the Ancell-Teicher Research Foundation for Genetics and Molecular Evolution for their support. Partly supported by the Ethologische Gesellschaft e. V.

Zusammenfassung

Allozymatische Divergenz und Systematik der Graumulle (Cryptomys, Bathyergidae, Rodentia) aus Sambia

Allozymatische Divergenz (34 Genloci) wurde bei zwei Populationen von afrikanischen Graumullen (*Cryptomys*) aus Sambia untersucht. Diese Untersuchung stellt damit die erste genetische Studie von Graumullpopulationen dar, die von außerhalb der südafrikanischen Region stammen. Zum Vergleich wurden parallel Allozyme (25 Loci) bei *Cryptomys damarensis, C. hottentotus, C. natalensis* aus Südafrika neu analysiert. Eine in früheren Studien schon festgestellte Dichotomie zwischen *C. damarensis* einerseits und *C. hottentotus* und *C. natalensis* andererseits wurde bestätigt. Die zwei untersuchten sambischen Populationen stellen zwei gute biologische Arten dar, die von allen drei südafrikanischen Arten spezifisch unterschieden sind. Sambische *Cryptomys* zeigen eine nähere Verwandtschaftsbeziehung zu *C. damarensis* als zu beiden anderen Arten. Die allozymatischen Befunde und deren Interpretation werden durch den Vergleich mit einigen anderen biologischen Aspekten bestätigt. Es wird gezeigt, daß die morphologischen Kriterien, die zur Zeit für die systematische Bewertung von *Cryptomys* benutzt werden, offensichtlich nicht ausreichend sind und daß eine moderne, breit angelegte Revision der gesamten Gattung notwendig ist.

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Authors' addresses: Maria Grazia Filippucci, Department of Biology, University of Roma "Tor Vergata", Via E. Carnevale, I-00173 Roma, Italy; Hynek Burda, Department of Morphology, Johann-Wolfgang-Goethe-University, Theodor-Stern-Kai 7, D-60596 Frankfurt am Main, FRG; Eviatar Nevo, Institute of Evolution, University of Haifa, Mt. Carmel, Haifa 31999, Israel; Jiri Kocka, Surgery Department University Teaching Hospital, P.O. Box 50001, Lusaka, Zambia

Z. Säugetierkunde 59 (1994) 52–57

ISSN 0044-3468

Habitat segregation of three sympatric fossorial rodents in the Spanish Pyrenees

By C. E. Borghi, Stella M. Giannoni, and J. P. Martínez-Rica

Instituto Pirenaico de Ecología, Jaca, Spain

Receipt of Ms. 16.4.1992
Acceptance of Ms. 2.12.1992

Abstract

Studied the microhabitat selection among three species of sympatric fossorial voles of the subgenus *Terricola* above the timberline in the Spanish Pyrenees. The intensity of habitat use in each plot was estimated by means of the capture data and by counts of mounds made by the fossorial activity of each species. Environmental features were measured and related to the occupation level of each species by means of correlations and correspondence analysis. Results reveal some segregation between the three species in factors such as soil thickness and percentage of plant cover. *Microtus pyrenaicus,* an endemic species, prefers deep soils and dense plant cover, while *M. duodecimcostatus* seems to avoid plots with many large rocks, high slopes and prefers dense plant cover, and *M. lusitanicus* prefers low plant cover and shallow soils.

Introduction

It is generally accepted that the diversity of subterranean mammals in a given area is low, and that different species are distributed among particular habitats according to the distribution of the limiting resources (Nevo 1979). From these premises and from several considerations of the environmental features of the underground environment, Nevo (1979) predicts that no substantial overlap occurs between fossorial mammals habitats; and when two or more species coexist, the should have at least different food needs, decreasing in this way interspecific competition. Spatial coexistence among fossorial mammals would be then possible only between herbivores and insectivores (Nevo 1979).

However, instances are known of the coexistence of fossorial mammals of the same general diet, within the same order, and even the same family. For instance, fossorial mammals such as some Chrysochloridae and Bathyergidae may be found together, even in the same burrows (Hickman 1990).

Many studies have investigated the microhabitat segregation of sympatric "above-ground" small mammals (e.g. Brown and Liebermann 1973; M'Closkey and Fieldwick 1975; Dueser and Shugart 1978; Stamp and Ohmart 1978). However, to our knowledge, the only studies concerned with microhabitat segregation of subterranean mammals are those of Reichman and Jarvis (1989) and Comparatore et al. (1992). The main conclusion of the former studies is that microhabitat segregation mainly depends on the plant biomass above their burrows in the case of the three species of bathyergids (Reichman and Jarvis 1989) and on the types of soil and vegetation in the case of the two species of the genus *Ctenomys* (Comparatore et al. 1992). On the other hand, in the subterranean environment on the mountains above timberline, some other environmental resources may explain the microhabitat segregation between coexisting sympatric species of the subgenus *Terricola.*

The objective of this study was to examine the coexistence of three very similar species of fossorial rodents, *Microtus pyrenaicus, M. lusitanicus* and *M. duodecimcostatus.* All of them coexist in the supraforestal level, have similar body size, and are herbivorous species.

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Material and methods

Study area

The study plot is located in the Spanish Pyrenees, not far from the small town of Jaca, at an altitude of 2000 m above sea-level (masl), at a site where the three-mentioned species coexist. The area consists of a plot, 100 m each side on a moderate slope with a grass cover of *Trifolium alpinum, Festuca rubra* and *Nardus stricta.* The area is covered with snow between November and June of every year.

Habitat selection

The plot was subdivided into 100 squares of 10 × 10 m. Pine voles were captured alive with traps of the Sherman type and the environmental features were recorded. Data were obtained during the summers of 1990 and 1991, periods when the study area was free of snow.

The intensity of habitat use in each subplot was estimated by means of direct methods: capture data, and by indirect methods: counts of mounds made by the fossorial activity of every species. Indirect methods of investigation are needed because of the difficulty in investigating fossorial rodents in a complex habitat such as in a soil environment (Reichman and Jarvis 1989). Environmental variables recorded were: soil thickness, slope, plant cover, area covered by rocky outcrops, mean stone diameter and the percentage of wild boar rooting.

Variables were analysed by means of univariate and multivariate statistics. Correlation between habitat variables and the number of mounds at each sample plot were tested by Spearman's rank correlation coefficients (Siegel 1986) because distributions of values were not normal. We have applied a correspondence analysis for the segregation of the different species. Habitat variables were subdivided into a number of categories. Subdivision of a parameter was determined by arbitrary evaluation of the width of the ecological gradient existing in the study area. A contingency table was created by expressing habitat variables as frequencies of occurrence of *Microtus* species. Calculation was based on the program SYN-TAX III/PC (Podani 1988).

Results

Spearman correlations

Total number of captured voles was 107 (65 *Microtus pyrenaicus,* 27 *M. duodecimcostatus* and 15 *M. lusitanicus*); 1153 soild mounds were found within the plot; from these, 393 were made by *M. pyrenaicus,* 640 by *M. lusitanicus* and 120 by *M. duodecimcostatus.*

Before any other analysis, we compared the capture level and the number of earth mounds on each subplot, as a way of calibrating the two estimates of habitat use. Both

Spearman rank correlation coefficients between habitat variables and number of mounds at each plot

(n = 1153)

Species	*M. pyrenaicus*		*M. lusitanicus*		*M. duodecimcostatus*	
	r_s	p	r_s	p	r_s	p
Number of mounds of *M. p.*	1.0000	1.0000	−0.2694	0.0073**	0.0420	0.6760
Number of mounds of *M. l.*	−0.2694	0.0073**	1.0000	1.0000	−0.0733	0.4665
Number of mounds of *M. d.*	0.0420	0.6760	−0.0733	0.4655	1.0000	1.0000
Average soil depth	0.3527	0.0004***	−0.0695	0.4894	0.0992	0.3236
Maximum soil depth	0.2267	0.0241*	−0.0136	0.8920	0.0841	0.4028
Minimum soil depth	0.3040	0.0025**	−0.0737	0.4631	0.1507	0.1337
% cover of exposed rock	−0.1685	0.0936	0.0514	0.6088	−0.2508	0.0126*
Average slope	−0.1466	0.1447	−0.0948	0.3457	−0.1849	0.0658
% cover of vegetation	0.3658	0.0003***	−0.3679	0.0003***	0.0921	0.3595
% cover of wild boar rooting	−0.0981	0.3293	0.5309	0.0000****	−0.0615	0.5407
Average diameter of rocks	0.1452	0.1485	−0.0627	0.5325	−0.2526	0.0120*

**** $p < 0.0001$; *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

variables were highly correlated (r_s = 0.48; $p < 0.0001$; n = 100). The low value of the Spearman coefficient may be due to the different time scale of both variables: while capture numbers reveal pine vole activity over a short span of time, the number of soil mounds is a cumulative variable related to the average habitat use during a long period. The second variable is preferred for habitat studies. The results of the correlation between variables are summarized in the table.

Microtus pyrenaicus

Habitat use of this species is positively correlated to plant cover (r_s = 0.37; $p < 0.0001$) and to soil depth (r_s = 0.35; $p < 0.0001$). Negative but not significant correlation exists between slope (r_s = −0.15; p = 0.14) and percentage of rocks in the subplot (r_s = −0.17; p = 0.09). It appears as if this species selected the best places to burrow, where soil is deeper and flatter, but, although several variables seems linked to this species, not one of them shows a correlation strong enough to allow prediction of the presence of the species as a function of only this variable. Therefore, the distribution of *Microtus pyrenaicus* should depend on an interaction between the four above-mentioned variables. Influence of different variables can be clearly seen in the figure. While the species seems to prefer lower slopes, it is found also in steep places, with slopes surpassing 40 %.

Microtus lusitanicus

The only positive correlation shown by this species is to the percentage of wild boar rooting (r_s = 0.53; $p < 0.0001$). A negative correlations exists between abundance of the species and plant cover (r_s = −0.37; $p < 0.01$).

Moreover, *M. lusitanicus* is negatively correlated to the abundance of *M. pyrenaicus* (r_s = 0.27; $p < 0.01$). It appears as if *M. lusitanicus* chose, or was forced to select, marginal habitats, not preferred by the former species. Association between this species and patches of wild boar activity is striking. Even where these patches do not coincide with active vole colonies there are signs of an old deserted colony of *M. lusitanicus*. Wild boar could be a predator of voles, and seems to prefer this species, due perhaps to accesibility offered by the more superficial burrows that *M. lusitanicus* makes.

M. lusitanicus inhabits sites with shallow soils, low proportion of rocky outcrops, high slopes and medium to sparse plant cover (Fig.).

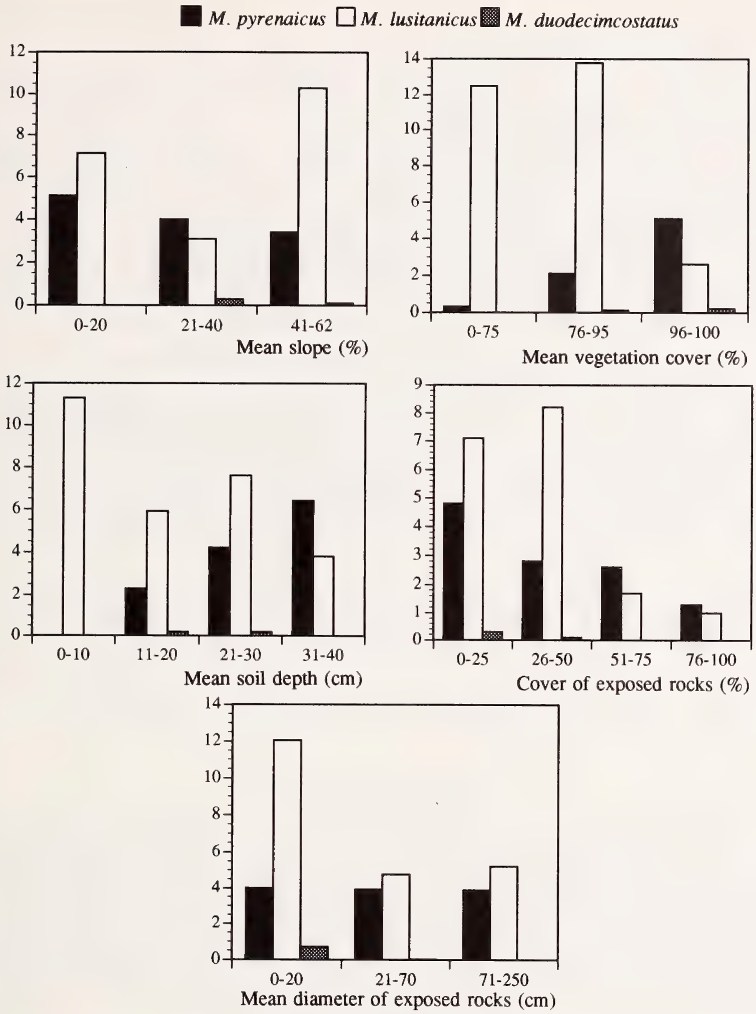
Microtus duodecimcostatus

This is a lowland species which in the study area almost reaches its altitudinal limit. It occurs in low abundance, and the number of both captures and mounds is small. The only significant correlations are negative, and rather low: there is a negative relationship between the abundance of the species and both the surface covered by rocks (r_s = −0.25; p = 0.012) and the average diameter of rock outcrops (r_s = −0.25; $p < 0.05$). As seen in the figure, the species seems to select soils of intermediate thickness, low presence of rocks, moderate slope and dense plant cover.

Correspondence analysis

The first axis explains approximately 81 % of the variance, and the first two axes accounted for the total inertia (100 %). The first axis seems to be linked to plant cover and soil thickness; the second axis is not so clear as the former one, and seems to be linked to the percent of rock outcrops and to gravel diameter. Wild boar rooting activity seems also linked to the first axis.

The first axis segregates the three species along the variables related with the slope, plant



Mean number of mounds in each plot, in Los Lecherines (2000 masl) related to the environmental features recorded

cover and soil depth, pointing to *M. pyrenaicus* as the species that can live in intermediate conditions, *M. duodecimcostatus* being associated with the deeper soils, and the highest values of plant cover; and *M. lusitanicus* associated with the opposite values of this axis. The second axis segregates *M. pyrenaicus* from the other species, *M. pyrenaicus* being the species that can live in plots with abundant and sizeable rocks, while the other species are associated with the opposite values of this axis.

Discussion

Microtus pyrenaicus appears to be rather flexible in its habitat use, being found at sites with very different features. *M. lusitanicus* is relegated to the thinnest soils and to sites with sparse plant cover, while *M. duodecimcostatus* is found only in the opposite microhabitats,

associated with high scores of plant cover and soil thickness, and with low slopes. The first species is also the only one that tolerates the use of rocky terrain.

Habitat segregation in sympatric fossorial mammals does not always rely on the partitioning of food resources, as implied by Nevo (1979). The unexpected spatial overlapping among three species of taxonomically related fossorial voles in the suprafores-tal level of the Spanish Pyrenees, and the three sympatric species of molerats in the Cape Province of South Africa (Reichman and Jarvis 1989) are a clear contra-example.

Our results suggest that *Microtus pyrenaicus* selects advantageous sites for burrowing, where soil is deep and flat. *M. duodecimcostatus* occurs at sites where competition with other species is low, or where environmental features are still adequate (thick and flat soil also), and *M. lusitanicus* at sites where the plant cover is sparser and where there are fewer interactions with *M. pyrenaicus. M. lusitanicus* is strongly associated with the activity of the wild boar, probably because it is most preyed on by the wild boar, in turn, perhaps due to its burrowing in the shallowest soils.

The highly complex topographic relief of the mountain environment produces an increase in diversity of mammalian species, as has already been observed for mammals in the United States (Simpson 1964), and particularly the epigeal *Microtus* species in North America (Rose and Birney 1985). The coexistence of three sympatric fossorial rodents in the Spanish Pyrenees could, therefore, be the final product of a very complex subterranean environment in the mountains, where soil depth, plant cover and slopes are very heterogeneous. The underground environment is very different to that of *Spalax ehrenbergi* studied by Nevo (1979) in arid environments, where the underground habitat is structurally simple, and where the competition for food resources may lead to competitive exclusion. Thus, an increase in complexity of the underground environment at high altitudes allows the sympatry of the pine voles, while the most important variables segregating the microhabitat of these species are soil depth and plant cover.

Acknowledgements

C. E. Borghi received a research grant within the framework of the CSIC-CONICET agreement between scientific institutions of Spain and Argentina; S. M. Giannoni had a research grant from the Instituto de Estudios Altoaragoneses, Spain; and the financial support was supplied from the project "Erosion in deserted fields" of the Spanish CICYT. This study will be a portion of a doctoral thesis of the first author. We would like acknowledge the help received from R. Soriguer (Estación Biológica de Doñana, Sevilla), R. Antor, G. del Barrio, D. Gómez, and J. Isern (Instituto Pirenaico de Ecología, Jaca). A. Danson assisted us with the English version. The critical comments of J. Telleria, M. Alcántara, S. Montalvo, J. Potti and anonymous reviewers helped to improve the manuscript greatly.

Zusammenfassung

Habitatwahl bei drei Arten von Kurzohrmäusen in den spanischen Pyrenäen

Drei Arten von Kurzohrmäusen, die in den spanischen Pyrenäen oberhalb der Baumgrenze syntop vorkommen, wurden auf Unterschiede in der Wahl des Lebensraumes hin untersucht. Die Dichte jeder Art in den Probeflächen wurde anhand der Mittelwerte von Fängen und der Anzahl aufgeworfener Hügel abgeschätzt. In den gleichen Probefeldern wurden verschiedene Umweltmerkmale registriert und mit den Vorkommenshäufigkeiten der drei Arten verglichen. Die Ergebnisse zeigen deutliche Unterschiede, vor allem in den Variablen Bodentiefe und Pflanzenbedeckung. *Microtus pyrenaicus*, eine endemische Art der Pyrenäen, bevorzugt tiefen, erdreichen Boden mit hoher Vegetationsdichte. *M. duodecimcostatus* scheint in Gebiete mit groben Felsen, stark abschüssigen Hängen und Gegenden mit hoher Vegetationsdichte auszuweichen, während *M. lusitanicus* anscheinend Flächen mit geringer Vegetationsdichte und flachgründigen Böden aufsucht.

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Authors' addresses: CARLOS E. BORGHI, STELLA M. GIANNONI, IADIZA-CRICYT, Casilla de Correo 507, RA-5500 Mendoza, Argentina, and JUAN P. MARTÍNEZ-RICA, Instituto Pirenaico de Ecología. Apdo. 64, E-22700 Jaca, Huesca, Spain

Z. Säugetierkunde 59 (1994) 58–60

ISSN 0044-3468

WISSENSCHAFTLICHE KURZMITTEILUNG

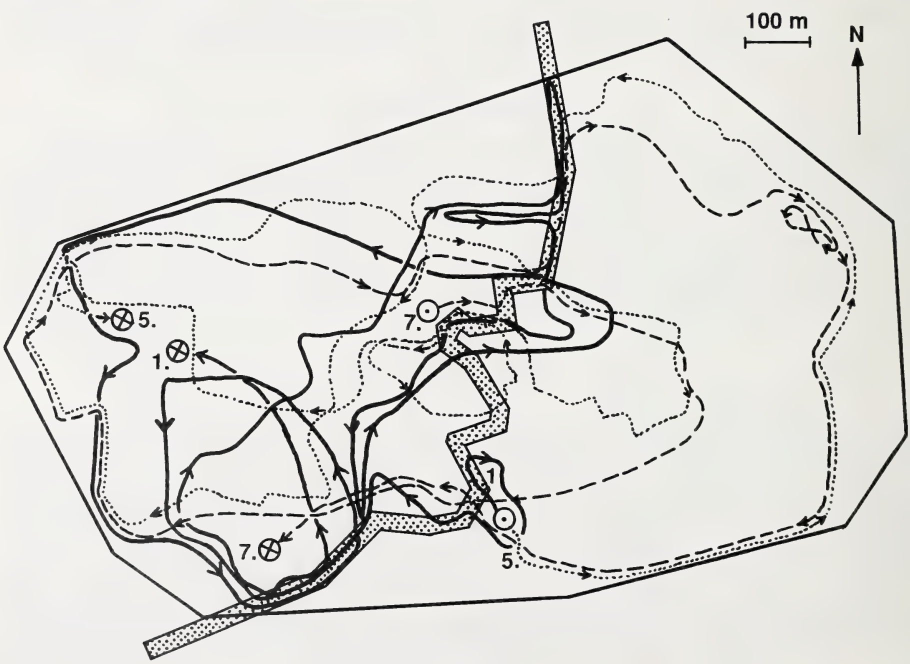
Reaction of a male Stone marten (*Martes foina* Erxleben, 1777) to foreign faeces within its territory: a field experiment

By A. Seiler, H. H. Krüger and A. Festetics

Institut für Wildbiologie und Jagdkunde, Göttingen, Deutschland

Receipt of Ms. 26. 7. 1991
Acceptance of Ms. 29. 7. 1993

The use of faeces and urine for marking territories, revealing sex and reproductive status, is widespread among carnivores (Gorman and Trowbridge 1989; Macdonald 1980). Stone martens scent mark their territories by exposing special small droppings and urinating on conspicuous locations (Grünwald 1988). They are territorial against conspecifics of the same sex (Krüger 1989) and increase their marking activity during the mating season (Grünwald 1988). Here, we report on an experiment, where we simulated the intrusion of a foreign male stone marten into the territory of a resident male during the mating season.



Examples of ranging movements of the male stone marten within its home range (convex polygon). The dotted lines represent movements during the nights 5. (19 June) and 7. (25 June) before; the thick solid line represents night 1. (26 June) after the exposition of conspecific faeces. The faeces were placed along the "olfactory corridor" (hatched area). ⊙ = start, ⊗ = end of one nightly movement

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The resident stone marten was trapped in June 1989 in the village of Hardegsen, near Göttingen, German Federal Republik (51°57′ N, 9°60′ E). It was fitted with a radio collar (Karl Wagener, Colonia) and tracked on foot and by bicycle continuously during its active time for the next five weeks. Tracking data was complimented with direct observations. Faeces of captive male stone martens (from the "Arbeitskreis Wildbiologie, Giessen") were mixed with water and spread out on a line through the home range. The suspension was renewed prior to every tracking night. A 25 m broad stripe along this line was defined as the "olfactory corridor", where the marten was regarded as having direct contact with the faecal scent (Fig.). We compared the marten's locomotoric activity (travel distance and speed) within the corridor before and after placement of the faeces. A total of 14 nights of observation were used for the analysis, 7 nights to document movement pattern and home range size and 7 nights for the experiment.

During the first period, the male ranged over nearly the whole village and moved often along the outer limits of his territory (Fig., convex polygon, minimum area = 65.7 ha). After placement of the faecal suspension, however, he mated with a female and spent a significantly higher proportion of his activity in the olfactory corridor (+75.4 %, one tailed Mann-Whitney U-test: $U = 39.5$, $df = 13$, $p = 0.027$, Tab. 1). This reduced his range to the inner and western part of his territory (Fig.), but did not affect his overall travel rate (Tab.).

During the first night after the placement, 26 June, the male encountered the corridor 10 times, moved within it over about 1.6 km, but 4 times he turned around immediately and ran back. In the second night, 27 June, after leaving his hiding place, he run directly to the corridor, sniffed the faeces and deposed a scent mark himself, showing the typical behaviour that Gründwald (1988) described for marking with urine. During the next 65 minutes he followed the corridor intensively over ca. 900 meters and sniffed several times

Travel distance (TD) and travel rate (TR) of a free living male stone marten throughout its territory and within the olfactory corridor, before and after placement of the foreign conspecific faeces

Date	Observation time (min.)	TD in total (m)	TD in corridor (m)	TR in total (m/min.)	TD in corridor /total TD (%)
Before					
1. 8 June	195	3930	250	20.2	6.4
2. 10 June	270	5470	350	20.3	6.4
3. 12 June	170	4590	1125	27.0	24.5
4. 14 June	180	5560	700	30.9	12.6
5. 19 June	135	2970	550	22.0	18.5
6. 22 June	90	3170	150	35.2	4.7
7. 25 June	250	4580	200	18.3	4.4
Average	184.3	4324.3	475.0	24.8	11.1
After					
1. 26 June	315	6840	1625	21.7	23.8
2. 27 June	120	3780	925	31.5	24.5
3. 28 June	284	8330	2225	29.3	26.7
4. 30 June	120	3730	425	31.1	11.4
5. 2 July	105	2840	425	27.0	15.0
6. 4 July	290	5650	1500	19.5	26.5
7. 5 July	287	4370	350	15.2	8.0
Average	217.3	5077.1	1067.9	25.1	19.4*

* The difference between the periods is significant according to a one tailed Mann-Whitney U-test: $U = 39.5$, $df = 13$, $p = 0.027$.

along the outspread suspension. Then he returned to his hiding place and was observed mating with a female, who probably lived in the western part of his territory. In the third night, 28 June, the marten was especially active, moved over 8 km and investigated the olfactory corridor very intensely (Tab.). In the following nights, the marten concentrated his movements again on the western part of his home range, but encountered the corridor more seldom. No mating was observed during this time.

Oestrus females are considered to be the limiting resource for males of solitary carnivores (Sandell 1989). Hence, prior to copulation, resident males should gain more from keeping close to and defending their receptive females, than from patrolling their territories. In our experiment, however, the male increased his activity along the olfactory corridor, although he was mating in the second night of the experiment.

The stone marten was obviously attracted by the suspension of its conspecifics' faeces. A similar behaviour was described by Grünwald (1988) with captive stone martens. Her animals showed a 11.3-fold increase in their exploratory behaviour and locomotoric activity, when they encountered scent marks of foreign martens. This was interpreted as agonistic and curiosity behaviour induced by the olfactory marks. Especially during the mating season, the scent of a male conspecific within an occupied territory is likely to initiate aggressive behaviour of the territory owner. At other times of the year, when other resources are more prevalent, territorial scent marks might be less important (see Pulliainen 1982).

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Authors' addresses: Andreas Seiler, Swedish University of Agricultural Sciences, Department of Wildlife Ecology, Grimsö Wildlife Research Station, S-73091 Riddarhyttan, Sweden; Hans-Heinrich Krüger and Prof. Dr. Antal Festetics, Institut für Wildbiologie und Jagdkunde, Universität Göttingen, Büsgenweg 3, D-37077 Göttingen, Germany

MITTEILUNGEN DER GESELLSCHAFT

Einladung

Auf Einladung von Frau Dr. F. Spitzenberger, Wien, findet die 68. Jahrestagung der Deutschen Gesellschaft für Säugetierkunde e. V. von Sonntag, den 25. September, bis Freitag, den 29. September 1994, im Naturhistorischen Museum in Wien statt.

Vorläufiges Programm

Sonntag, 25. September:		Anreise
	ab 16.00 Uhr:	Vorstandssitzung im Naturhistorischen Museum, Burgring 7
	ab 19.00 Uhr:	Zwangloser Begrüßungsabend im „Gösser Bräu“
Montag, 26. September:	9.00 Uhr:	Hörsaal 1 im Biozentrum der Universität: Grußworte und Eröffnung der Tagung durch den 1. Vorsitzenden
	9.30 Uhr:	Hauptvortrag und Kurzvorträge zum Themenschwerpunkt „Holozäne und spätpleistozäne Säugetierfauna“
	14.00 Uhr:	Kurzvorträge
	16.00 Uhr:	Posterdemonstration
	17.00 Uhr:	Mitgliederversammlung
	19.00 Uhr:	Empfang im Naturhistorischen Museum
Dienstag, 27. September:	9.00 Uhr:	Hörsaal 1 im Biozentrum der Universität: Hauptvortrag und Kurzvorträge zum Themenschwerpunkt „Akustische Kommunikation und Gehör bei Säugetieren“
	14.00 Uhr:	Kurzvorträge
	16.00 Uhr:	Posterdemonstration
	17.00 Uhr:	Gemeinsame Abfahrt zum geselligen Abend beim Heurigen
Mittwoch, 28. September:	9.00 Uhr:	Hörsaal 1 im Biozentrum der Universität: Hauptvortrag und Kurzvorträge zum Themenschwerpunkt „Systematik und Ökologie ost- und südosteuropäischer Säugetiere“
	13.30 Uhr:	Posterdemonstration
	14.15 Uhr:	Posterprämierung und Abschluß des wissenschaftlichen Programms
	14.45 Uhr:	Gemeinsame Abfahrt zum Tiergarten Schönbrunn. Führung und Empfang durch den Tiergartendirektor Dr. H. Pechlaner.
Donnerstag, 29. September:	9.00 bis 17.00 Uhr	Exkursion zum Neusiedlerseegebiet. Vogelzug und Zieselkolonie, Führung durch die Biologische Station Illmitz
	9.00 bis 12.00 Uhr:	Kleiner Kurssaal im Naturhistorischen Museum: Symposium der „Arbeitsgruppe Biber“

Rahmenprogramm: Demonstration der Trainingsarbeit der Lipizzaner und Besichtigung der Kaiserappartements.
Alle Interessenten, Mitglieder und Nichtmitglieder, sind zu dieser Jahrestagung 1994 der Deutschen Gesellschaft für Säugetierkunde in Wien herzlich eingeladen. Falls eine persönliche Einladung gewünscht wird, wenden Sie sich bitte an den 1. Vorsitzenden der Deutschen Gesellschaft für Säugetierkunde, Prof. Dr. U. Schmidt, Zoologisches Institut, Poppelsdorfer Schloß, D-53115 Bonn (Tel. 02 28/73 54 68; Fax 02 28/73 54 58). Das Programm mit der Vortragsfolge wird den Mitgliedern – auf Anforderung auch Nichtmitgliedern – rechtzeitig vor der Tagung zugesandt.

Wir bitten um die Anmeldung von Tagungsbeiträgen. Außer Beiträgen zu den genannten Themenschwerpunkten werden dieses Mal wieder verstärkt Kurzvorträge und Posterdemonstrationen zu anderen Fachgebieten der Säugetierkunde berücksichtigt.

Bitte melden Sie Kurzvorträge (15 Min. + 5 Min. Diskussion) sowie Posterdemonstrationen möglichst frühzeitig, spätestens jedoch bis zum 30. April (Ausschlußfrist) beim Geschäftsführer der DGS, Prof. Dr. H. Erkert, Zoologisches Institut, Auf der Morgenstelle 28, D-72076 Tübingen (Tel. 0 70 71/29 29 58; Fax: 0 70 71/29 46 34) an. Der Anmeldung ist eine maximal einseitige informative Kurzfassung (1,5zeilig) beizufügen. Aus ihr sollen die Fragestellung, Methoden, Ergebnisse und die daraus gezogenen Schlußfolgerungen hervorgehen. Alle Kurzfassungen, die wieder in einem Sonderheft der Zeitschrift für Säugetierkunde publiziert werden sollen, sind nach dem folgenden, schon im letztjährigen Abstractheft eingeführten Schema abzufassen: Deutscher Titel, Leerzeile, englische Titelübersetzung (kleine Anfangsbuchstaben im Text; bitte ggf. einen „native speaker" konsultieren), Leerzeile, Initialen und Familienname(n) des/der Autors(in) bzw. der Autoren(innen) in Großbuchstaben, Leerzeile, Adresse, Leerzeile, Text (nicht formatiert). Aus arbeitsökonomischen Gründen bitten wir dringend darum, zusätzlich zu diesem ausgedruckten Abstract möglichst noch eine Fassung auf Diskette (5.25" oder 3.5", IBM-kompatibler DOS-PC) in Form eines Word- (5.0 oder 5.5) oder ASCII-Files mitzuschicken. Die Maße für Poster werden im Juni-Rundschreiben der DGS bekanntgegeben.

Mit Fragen zum Tagungsort und zur Organisation wenden Sie sich bitte an Frau Dr. F. Spitzenberger, Naturhistorisches Museum Wien, Postfach 417; A-1014 Wien, Österreich (Tel. 00 43/1 52 17 73 12; Fax: 00 43/1 93 52 54).

Internationales Symposium unter der Schirmherrschaft der DGS über "Current Problems of Bat Protection in Central and Eastern Europe"

Auf Einladung von Prof. Dr. U. Schmidt, Bonn, findet vom 22. bis 25. Juli 1994 im Zoologischen Institut der Universität Bonn ein internationales Symposium zum oben genannten Thema statt. Alle Interessenten sind dazu herzlich eingeladen. Auskunft erteilt Prof. Dr. U. Schmidt, Zoologisches Institut, Poppelsdorfer Schloß, D-53115 Bonn (Tel. 02 28/73 54 68; Fax 02 28/73 54 58).

European Squirrel Group

Die "European Squirrel Group" ist ein Zusammenschluß von Forschern aus überwiegend europäischen Ländern, die sich in ihren wissenschaftlichen Arbeiten mit Hörnchen beschäftigen. Die Schwerpunktthemen decken ein recht breites Feld ab, welches sich von Fragen zur Ökologie der verschiedenen Arten über morphologische und physiologische

Aspekte bis hin zur Populationsgenetik erstreckt. Auch Natur- und Artenschutzbelange nehmen einen breiten Raum ein.

Die Gruppe existiert seit etwa zwei Jahren. Regelmäßige Treffen in ein- bis zweijährigen Abständen sollen dem wissenschaftlichen Austausch dienen und die Kooperation fördern. Die nächste offizielle Zusammenkunft ist im Anschluß an den "II. European Mammal Congress" in England 1995 geplant.

Weitere Informationen sind zu erhalten bei: European Squirrel Secretariat, Luc Wauters, Dept. Biology, UIA, Universiteitsplein 1, B-2610 Wilrijk, Belgien, und Sibylle Münch, Lusenstr. 41, D-94556 Waldhäuser, Bundesrepublik Deutschland, Tel. (08553) 6515.

Seventy-Fifth Anniversary Meeting of the American Society of Mammalogists

The National Museum of Natural History and National Zoological Park, Smithsonian Institution, and the Biological Survey Section, National Biological Survey, are hosting the 75th Anniversary Meeting of the American Society of Mammalogists, to be held in Washington, D. C., 18–23 June 1994. Due to the commemorative nature of this year's annual meeting, there will be special symposia and integrated workshops that thematically address Biodiversity and Levels of Biological Organization, in addition to the usual schedule of technical sessions.

This is the final call for oral and poster presentations. There is space for a maximum of 97 oral presentations and 180 posters, allotted on a first-come, first-serve basis (i.e., data of postmark). All abstracts must be submitted by 1 March 1994, and accompanied by the preregistration form and registration fee. Questions concerning registration should by addressed to: Michael D. Carleton, Mammal Division MRC 108, National Museum of Natural History, Washington, D. C. 20560, USA (202-786-2490) or 357-1920; Fax 202-357-4779).

BUCHBESPRECHUNGEN

Ueckermann, E.: **Das Sikawild.** Vorkommen, Naturgeschichte und Bejagung. Hamburg und Berlin: Paul Parey 1992. 103 S., 45 Abb., 30 Tab. Kart. DM 16,–. ISBN 3-490-08812-3

In zweiter, neubearbeiteter und erweiterter Auflage liegt nun „Das Sikawild" als Heft 7 der Schriftenreihe der Forschungsstelle für Jagdkunde und Wildschadenverhütung des Landes Nordrhein-Westfalen vor. Ein wichtiger, auch im Untertitel genannter Aspekt dieser Abhandlung betrifft die Bejagung. Dieser Teil, der in die Kapitel Abschußplanung, Abschußdurchführung und Abschußrichtlinien sowie Bewertung untergliedert ist, richtet sich besonders an den Jäger und Forstmann und soll hier nicht weiter erörtert werden. Dagegen beanspruchen Vorkommen und Naturgeschichte dieser Wildart auch das Interesse des Säugetierkundlers. Zwar gibt es in der Bundesrepublik nur etwa 2000 freilebende Sikahirsche in einigen wenigen, voneinander isolierten Gebieten, und somit ist diese Art auf den ersten Blick nur von untergeordneter Bedeutung, doch als eingebürgertes Tier hat es zweifellos einen besonderen Stellenwert, vor allem unter den Gesichtspunkten der Einpassung in einen fremden Lebensraum und der Auseinandersetzung mit heimischen Arten. Hierzu fehlt noch eine umfassende Darstellung, doch teilt der Autor zahlreiche Einzelheiten mit; das betrifft die Beschreibung des natürlichen Areals der Art, ihrer Unterarten und deren Status sowie die Geschichte der Einbürgerung des Sikawildes sowohl in Deutschland als auch im weiteren europäischen Gebiet und darüber hinaus. Des weiteren erörtert er die Art und Weise der Einbürgerung in Deutschland und die Entwicklung der einzelnen Bestände unter Berücksichtigung ihrer Lebensweise; dabei geht er auch auf Krankheiten, Verluste durch den Straßenverkehr, durch dieses Wild verursachte Schäden und Bastardierungen ein.

Durch Abbildungen und Tabellen werden zahlreiche Sachverhalte veranschaulicht, ein Stichwortregister erleichtert die Benutzung des Buches, und ein umfassendes Verzeichnis führt den Leser zu weiterer Literatur über diese Hirschart.

D. Heinrich, Kiel

Wiesemüller, W.; Leibetseder, J. (Hrsg.): **Ernährung monogastrischer Nutztiere.** Jena, Stuttgart: Gustav Fischer Verlag 1993. 308 S., 39 Abb., 166 Tab. DM 128,–. ISBN 3-334-60428-4

Dieses Buch, an dem sieben Fachleute aus Deutschland und je einer aus Ungarn, Österreich und der Schweiz mitarbeiteten, wendet sich an jene, die Nutzsäugetiere gesund, ausgewogen, wirtschaftlich und mit möglichst geringer Belastung der Umwelt ernähren wollen. Es werden Leser angesprochen, bei denen die Kenntnis der Grundlagen der Tierernährung vorausgesetzt werden kann, also Tiermediziner, Ernährungsfachleute, Landwirte und Futtermittelproduzenten.

Zunächst wird ein Überblick über Fragen der Futtermittelkunde vermittelt. Dabei wird nicht nur kurz die Futtermittelanalyse, die energetische Futtermittelbewertung und das Futtermittelrecht abgehandelt, sondern es werden auch durch Futtermittel verursachte Schadwirkungen besprochen.

Auf den folgenden Seiten werden Informationen zur Ernährung des Hausschweins geboten, wobei nach einer Darstellung physiologischer Grundlagen gesondert Sauen, Ferkel, Zuchteber und Mastschweine berücksichtigt werden. Bei der folgenden Darstellung der Ernährung der Pferde werden zunächst die ernährungsphysiologischen Grundlagen und dann Besonderheiten des Verhaltens der Pferde gegenüber Mangel und Überschuß besprochen. Gesondert folgen dann praktische Hinweise zur Fütterung von Sportpferden, Zuchtstuten, Fohlen, Deckhengsten und Ponys sowie Empfehlungen zur Vermeidung ernährungsbedingter Krankheiten.

Die Ernährung des Kaninchens wird auf den folgenden Seiten abgehandelt, wobei in einem einleitenden Abschnitt auf die bei den Lagomorpha auftretende Zäkotrophie, die Aufnahme eines speziellen und im Blinddarm gebildeten Weichkotes, aufmerksam gemacht wird. Von vier ausgewählten Pelztierarten, wie Sumpfbiber oder Nutria, Nerz sowie Blau- und Silberfuchs wird die Ernährung behandelt, ferner die von Hunden und Katzen. Am Ende der genannten Abschnitte findet sich je ein Literaturverzeichnis. Diese Verzeichnisse sowie 166 außerordentlich materialreiche Tabellen, welche meistens übersichtlich gestaltet sind, erlauben es, den vorliegenden Band als Nachschlagewerk bei praktischen Fütterungsproblemen zu nutzen. Es erweist sich als sehr hilfreich und sollte anderen Buchautoren und Verlagen zur Nachahmung empfohlen werden, daß sich auf den Vorsatzseiten am Anfang des Bandes eine Liste der im Buch benutzten Abkürzungen befindet! Ein 16 Seiten langes Sachregister schließt das Werk ab.

Neben den eingangs genannten Interessenten dürfte dieses praxisbezogene Buch für Tiergärtner nützlich sein. Ferner macht der Band auch vergleichend interessierten Säugetierkundlern, Physiologen und Anatomen eine große Fülle von Daten leicht zugänglich, die in Spezialarbeiten und Monographien verstreut sind.

P. Langer, Gießen

Erscheinungsweise und Bezugspreis 1994: 6 Hefte bilden einen Band. Jahresabonnement Inland: DM 378,– zuzüglich DM 13,80 Versandkosten; Jahresabonnement Österreich: öS 2949,– zuzüglich öS 164,– Versandkosten; Jahresabonnement Schweiz: sfr 364,– zuzüglich sfr 21,– Versandkosten; Jahresabonnement EG-Binnenmarkt-Länder mit USt-ID-Nr.: DM 353,27 zuzüglich DM 19,63 Versandkosten; Jahresabonnement EG-Binnenmarkt-Länder ohne USt-ID-Nr. und Drittländer: DM 378,– zuzüglich DM 21,– Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey GmbH & Co. KG, Spitalerstraße 12, D-20095 Hamburg, Bundesrepublik Deutschland, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde" erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Z. Säugetierkunde 59 (1994) 1, 1–64

Vol. 59 (2), 65–128, April 1994 ISSN 0044-3468 C 21274 F

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde

Verlag Paul Parey Hamburg und Berlin

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

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Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Dieter Kruska.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologiezentrum der Christian-Albrechts-Universität, Am Botanischen Garten 9, D-24118 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

Fortsetzung 3. Umschlagseite

 Verlag: Paul Parey GmbH & Co. KG, Hamburg und Berlin. Anschriften: Spitalerstr. 12, D-20095 Hamburg; Seelbuschring 9–17, D-12105 Berlin, Bundesrepublik Deutschland. – Printed in Germany by Westholsteinische Verlagsdruckerei Boyens & Co., Heide/Holst.

Z. Säugetierkunde 59 (1994) 65–73

ISSN 0044-3468

Annual age structure and reproductive patterns in *Marmosa incana* (Lund, 1841) (Didelphidae, Marsupialia)

By MARIA LUCIA LORINI, J. A. DE OLIVEIRA, and VANESSA G. PERSSON

Museu Nacional, Universidade Federal do Rio de Janeiro; and Museu de História Natural "Capão da Imbuia", Curitiba, Paraná, Brazil

Receipt of Ms. 6. 1. 1993
Acceptance of Ms. 10. 2. 1993

Abstract

Investigated were the annual age structure and reproductive indicators in museum specimens of the mouse opossum *Marmosa incana*. Monthly distributions of relative age classes, indexed by tooth eruption and wear, suggest an almost total cohort turnover in an annual cycle (males: one year; females: one year and half). Analysis of tegumentary indicators of reproductive activity, gauged by examination of internal reproductive tracts, demonstrated that all the sexually matured individuals belong to the two oldest age classes. These populational features combined with a three-month seasonal breeding period, detected in the greater part of the geographic range of *M. incana*, apparently result in an unusual life history strategy for this species, characterized by only one "big-bang" reproductive event in a lifetime.

Introduction

Central to the distinction between marsupials and eutherians are the profoundly different morphologies and functions of the reproductive tracts (GRIFFITHS 1978). Likewise, there are marked differences in the early phases of development, marsupials lacking a true trophoblast and apparently not being able to provide prolonged protection for the genetically foreign embryo against the mother's immune system (LILLENGRAVEN et al. 1987). Such features determine a short gestation and a long lactation period, in which a major part of marsupial development is carried out. Together with the characteristically lower rates of development in marsupials (LEE and COCKBURN 1985), these reproductive characters strongly affect aspects of their populational biologies, especially the age of sexual maturation, litter size and litter frequency.

The greater part of what is known about the reproductive biology and life history of marsupials is based on studies focusing on the Australian forms. Contrastingly, detailed specific analyses of wild populations, such as those carried out upon Australian species (e.g. NEWSOME 1965; GUILER 1970; WOOD 1970; GEMMELL 1982), are still rare for the less diversified South American marsupials. To date, most of the reproductive information for the neotropical species comes from small mammal community mark-release studies (e.g. DAVIS 1946; REIG 1964; O'CONNELL 1979; FONSECA and KIERULFF 1989; STALLINGS 1989). In this approach there are usually two difficulties to be faced: the ageing of living specimens in the field and the virtual impossibility of examining the internal reproductive tracts of every individual, making it necessary to use indirect external evidence, such as tegumentary gland activity, to infer the reproductive condition of specimens. The precise correspondence between these indicators and the actual reproductive status, as well as the interspecific variation in their expression, has not yet been investigated.

Herein we propose an alternative approach to the study of reproductive and life history patterns of the didelphid marsupial *Marmosa incana* (mouse opossum), analysing the reproductive indicators in museum specimens for which real reproductive status and relative age are, at least in part, available. *Marmosa incana* shows three pelage types (A, B

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and C), unevenly distributed over the year, and apparently related to age, sex and sexual maturity (Oliveira et al. 1992). Such results suggested a detailed investigation of the monthly age structure and reproductive conditions in this species. Notable aspects of the reproductive biology and their bearing on the life history of this marsupial, so revealed, are described in the present contribution.

Material and methods

The total sample analysed in this study is composed of 311 museum specimens from eastern Brazil (Bahia, Minas Gerais, Espírito Santo, Rio de Janeiro and Paraná states), covering the greater part of the geographic range of *Marmosa incana*. Localities, sample sizes and museum acronyms were listed in Oliveira et al. (1992). Date of collecting, sex, body length, weight and conditions of internal reproductive tracts, when available, were taken from original labels. Specimens were aged on the basis of molariform tooth eruption (classes 1 to 6 as established by Tribe 1990) and five consecutive stages of M1–M4 wear, after complete positioning of PM3. The first two stages were allocated to age class 6 and the last three stages to age class 7 (Oliveira et al. 1992).

As a first step toward understanding the age and seasonal distribution of *M. incana*, we tabulated the occurrence of all individuals with sex and age class available (n = 225) by month of collecting.

Regarding the female reproductive condition, color change in the pouch or mammary region is commonly used as an indicator of breeding activity in living didelphids. In some species of *Marmosa* an orange to rust-brown stain around the mammary area is produced during pregnancy and nursing (Barnes 1977). We investigated the occurrence of this stained area and the degree of development and degeneration of nipples in *M. incana* and related these features to reproductive data available from some specimens to infer the females' reproductive condition.

The sternal gland area, a field of hypertrophied apocrine sudoriferous and sebaceous glands (Barnes 1977), was also investigated in each specimen. The activity of these glands has been referred to in the literature as associated with territorial marking and reproductive activity in some species of *Marmosa* (Hunsaker II and Shupe 1977); sternal gland activity is characterized by an oily secretion which dries to an amber to dark brown deposition attached to the skin, forming a concretion above the gland field that often glues hairs together.

Results and discussion

Age structure

Analysis of the age composition by month (Fig. 1) reveals that age classes are not homogeneously distributed over the year. Young individuals (classes 3 and 4) are restricted to between January and May in all localities except Ilhéus (state of Bahia), where one additional specimen was collected in September. Class 5 appears in February and occurs until May, with one exception in August for the Ilhéus population. Disregarding these two exceptional individuals from Ilhéus, age classes 3, 4 and 5 are distributed in a restricted and almost coincident period. From class 6 on, differences between sexes are noted in the monthly distributions. Whereas males of class 6 are present from February to October, with higher frequencies between April and May, females appear from April to November, and are more frequent between July and August. Frequency of class 6 increases by the middle of the year, when class 5 declines. Similarly, frequency of class 7 increases in the last months of the year, while frequency of class 6 declines.

Distribution of class 7 over the year extends for ten months for females and eight months for males. Except for two individuals from Ilhéus collected in April, males of age class 7 are absent from February to May. Females of this age class do not occur between July and August, except for one individual from Ilhéus, trapped in July.

It is relevant to note that exceptional individuals reported above comprise only 8 % of the total sample with available data on sex, age and month of capture from Ilhéus (n = 62).

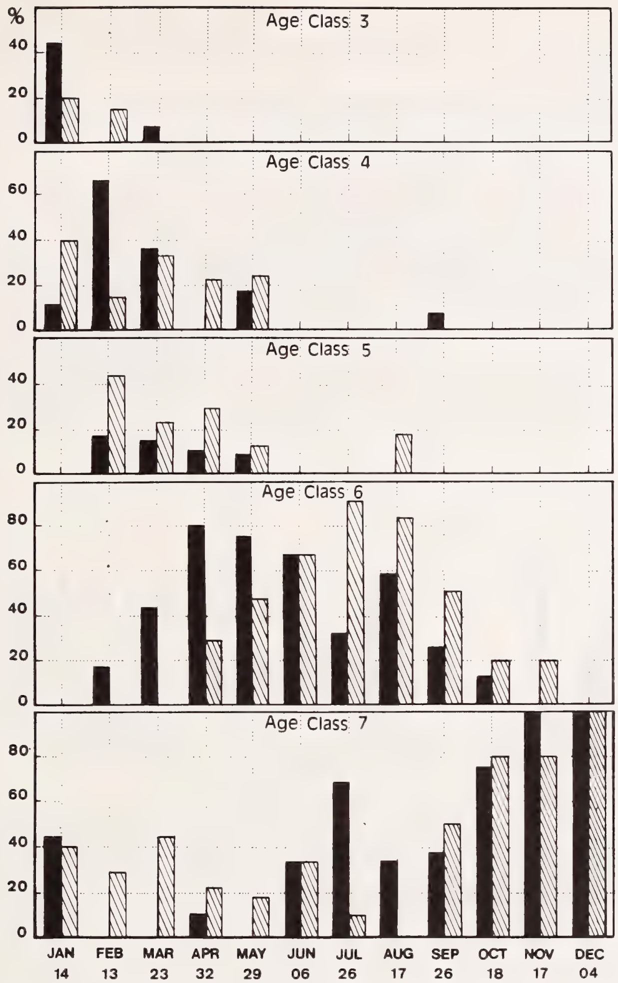

Fig. 1. Monthwise age distribution of *Marmosa incana*. Black bars: males; striped bars: females

Analysis of the mammary region

Analysis of the mammary conditions revealed that females of age classes 3, 4, 5 and 6 with long and soft pelage (type A) did not show indications of reproductive activity. All reproductive females belong to age classes 6 and 7, and have short and coarse pelage (type B).

Six different conditions of the mammary region were identified: a. not stained, indistinguishable from the rest of ventral pelage; b. not stained, but showing glabrous circles without teats; c. stained, showing conspicuous glabrous circles around incipient teats; d. stained, with a homogeneous set of cylindrical nipples up to 1 mm in diameter, each one inside a well-defined glabrous area; e. stained, with a heterogeneous set, containing some lax nipples (more than 1 mm in diameter) and others showing various stages of degeneration, in some cases reduced to a scar; f. stained, showing only darkened scars, with inconspicuous glabrous areas. Reproductive data described in the labels and the analysis of the internal reproductive tracts of recently collected specimens permitted us to

allocate the females, assigning each of the six conditions described above to their respective stages: non-reproductive (a); pre-reproductive (b); pregnant (c), early lactant (d), late lactant (e), and post-lactant (f).

All reproductive females presented a stain in the mammary region. However, even the post-lactants showed the mammary stain, an indication that it remains in the integument as a residual.

This feature has often been employed to determine the reproductive period in *Marmosa incana* (Fonseca and Kielruff 1990; Stallings 1990). However, this indicator alone does not provide a specific identification of the various reproductive phases of females, since in marsupials the nursing period is extended. Marsupials are born in an exceptionally altricial state, and a large part of their development takes place while fused to or dependent on a nipple.

Monthly rates of reproductive females (Fig. 2) revealed that periods of pregnancy, early and late lactancy, and post-lactancy are consecutive and seasonally distributed over the year. Pregnant females are limited to November, except for one individual collected in

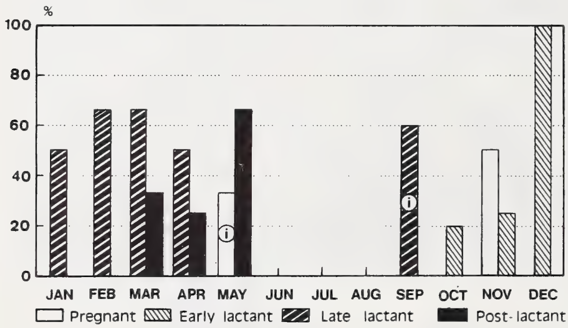

Fig. 2. Monthwise distribution of female reproductive status. Frequency of each status in relation to the total of females showing pelage type B. Bars marked with i denote exceptional individuals from Ilhéus

May in Ilhéus. Early lactant females were captured between October and December, and late lactants between January and April, except for three individuals from Ilhéus collected in September. Post-lactant females are restricted to the period from March to May in the total sample.

Reproductive period

Analysis of the annual distribution of female reproductive status, together with the occurrence of offspring made it possible to identify the reproductive period for *M. incana.* Distributions of pregnant and lactant females suggest that the mating period and subsequent teat attachment phase occur between October and December in the total sample except for part of the Ilhéus population, where a pregnant female was captured in May.

The limited distribution of the youngest individuals in our sample (age class 3) is independent evidence of a single and seasonal three-month reproductive period for the total sample, except the Ilhéus population, where an additional mating period is revealed in May. The distributions of juvenile ages (classs 3 and 4) are coincident with the January–April distribution of late lactant females.

The annual distribution of post-lactant females is coincident with the last months of occurrence of age classes 4 and 5. A comparison of our results with the development data obtained for *Marmosa robinsoni* (Eisenberg 1981; O'Connell 1983) makes it possible to relate the juvenile dental age classes 3, 4 and 5 with the rear cycle phases. Age class 3 individuals are probably in the nest phase, when the young of *M. robinsoni* begin to eat solid food and are able to leave the nest alone or following the female (O'Connell 1983). Classes 4 and 5 are correlated with the weaning and dispersion events. This conclusion is in

keeping with the attainment of a total crushing surface with four functional molariform teeth at these ages.

The reproductive period is probably more restricted in a given locality than the three months obtained in our analysis, and some asynchrony among localities is not unexpected at all, since reproductive patterns are influenced by local conditions. Among enviromental factors that have been recognized in the determination of the reproductive patterns in didelphid marsupials is the seasonality of rainfall (O'CONNELL 1979).

Our total sample comprises several series collected in various parts of the state of Minas Gerais which show a comparable pattern of rainfall, with five to six drier months in the year, and a sample from Ilhéus, in the state of Bahia, a locality characterized by the absence of a dry season (NIMER 1989). Additional records are from localities in Rio de Janeiro, Espírito Santo and Paraná states, in which rainfall distributions show an intermediate pattern as compared to Minas Gerais and Ilhéus.

The reproductive period revealed by our analysis corresponds very well to the rainy season in all localities of Minas Gerais, which compose the greater part of our sample. Remaining localities do not show inconformity to the Minas Gerais pattern, except Ilhéus. In fact, more than one reproductive period in the Ilhéus population is attested by the occurrence of a pregnant female in May and exceptional young individuals of age classes 4 and 5 (August–September), together with a single late lactant female in September.

Consequently, at least two reproductive periods in the year are revealed in the analysis of the Ilhéus sample. A major one, coincident with that shown by the total sample (October–December), and another, revealed by a smaller number of individuals, occurring from March to May.

Sexual maturity

Further interpretation of the results described above, together with that of pelage variation in *Marmosa incana* (OLIVEIRA et al. 1992), permits a determination of the sexually matured individuals. Since TATE (1933), it has been widely accepted that sexual maturity in *Marmosa* is attained at an early stage of life, when the last molariform tooth (third premolar for *M. incana*) is beginning to erupt, a stage that corresponds to class five in our analysis. Our results do not confirm TATE's assertion, at least for *M. incana*. As can be inferred from figure 1, distributions of age class 5 and most of class 6 are not coincident with the reproductive period. Indeed, among females, individuals with reproductive indications were found only in the last two age classes (6 and 7), all showing the short and dull pelage previously described as type B (OLIVEIRA et al. 1992). Almost all males taken during the three months of the reproductive period (October–December) belong to age class 7. The attainment of sexual maturity in males was thought to occur in connection with pelage type C (OLIVEIRA et al. 1992). The monthly prevalence of males with conspicuous type C pattern (modified hairs reaching the middorsum) relative to the total of age class 7 and pelage type C (Fig. 3) demonstrates this relationship. Additional evidence of

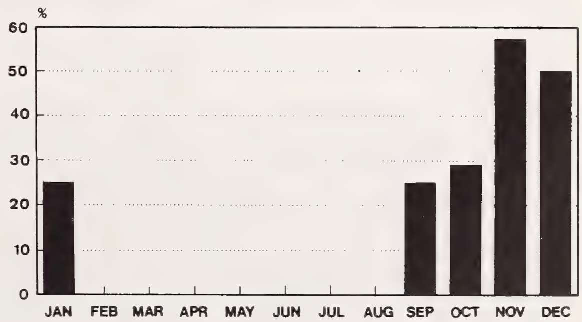

Fig. 3. Frequency of males with modified dorsal hairs reaching the middorsum in relation to the total age class 7 and pelage type C males

the strong correlation between the attainment of sexual maturity and pelage type C is provided by histological analysis of testes. Slides obtained from individuals of age class 7 and pelage type A did not reveal any spermatogenic activity (Oliveira et al. 1992).

The only exceptions to the limited distribution of pelage type C males over the year (July–January) are two individuals from Ilhéus collected in April (Oliveira et al. 1992), precisely during the additional reproductive period at this locality.

Analysis of sternal gland activity

Our results show that the sternal gland is externally discernible in the skins of both sexes at all ages analysed, contrary to Tate's (1933) and Hunsaker and Shupe's (1977) assertions that the gland is not present in *Marmosa incana*. Residuals of the oily secretion were detected in specimens of both sexes from class 4 onwards over the year. Frequencies of individuals with sternal secretion by age classes attest to a similar pattern between males and females, with a clear peak in activity at age class 5 and a succeeding decrease at class 6 (Fig. 4). At age class 7, on the other hand, almost all males show glandular activity, whereas females continue with a low percent of individuals showing sternal gland secretion.

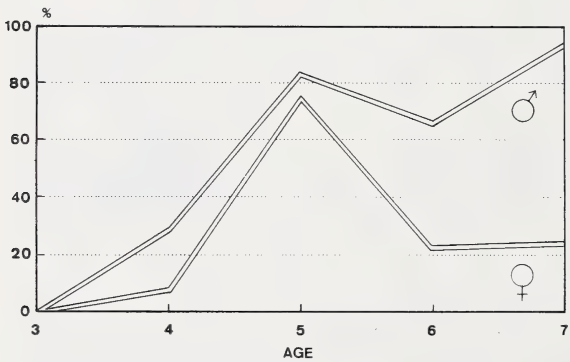

Fig. 4. Frequency by age of individuals showing sternal gland activity

These results do not point to an unequivocal correspondence between the occurrence of sternal gland secretion and reproductive activity. The increasing frequency of sternal secretion in both sexes at classes 4 and 5 (Fig. 4), probable ages of juvenile independence, may be related, rather, to dispersion behavior.

Semelparity

The absence of class 7 males between February and May in all localities except Ilhéus cannot be accounted for by small sample sizes, as even at Além Paraíba (Minas Gerais), where a large sample from these months was assembled (n = 64), no males of age class 7 were obtained.

After the absence period (February–May), the only male of class 7 registered in June and most of age class 7 males that were gathered in July show pelage type A. Mean weight of specimens collected between June and August, the first three months after the absence period, is lower than that from the three months before the males' disappearance (November–January). In the same way, molar wear is more accentuated among class 7 before the absence period, suggesting that the males which disappear after January and those collected after June do not belong to the same generation.

In regard to females, the absence of age class 7 in July and August may also be evidence

Descriptive statistics of body weight for samples of supposed cohorts in each sex

Within parenthesis, f-ratio and associated probability (ANOVA) for the null hypothesis of no difference between samples from after (a) and before (b) adults' disappearence

	Males		Females	
	(a) Jun–Aug	(b) Nov–Jan	(a) Sep–Nov	(b) Mar–Jun
n	11	13	16	10
min–max	35–97	50–120	30–62	48–66
mean	60.4	88.4	46.3	58.3
sd. dev.	21.2	18.7	10.2	6.8
(F-ratio)	(11.86)		(10.66)	
(P)	(0.002)		(0.003)	

of a gap between two successive generations. The mean weight of females collected after these months is also lower than that from the first semester, and the molar wear is less accentuated.

Analysis of variance, employed to test the null hypothesis of no differentiation between samples of these supposed cohorts, also revealed that differences in mean weight were significant at the 1 % level ($P < 0.01$) for both sexes (Table).

A probable explanation for the males' absence may be related to a general mortality after the reproductive period. Similarly, the results set forth above also show that females which had already reproduced are not present in a new reproductive period in the following year. Since for females the gap between generations is shorter, it might be supposed that occasionally a female would reach the breeding season of the next year. However, data from *Marmosa robinsoni*, a species of similar habits and size, do not support the hypothesis that such a female would be reproductive, since females of that species are no longer fertile after 17 months.

To date, *M. robinsoni* is the only mouse opossum for which comprehensive reproductive data is available. Young individuals of this species are completely weaned 65 days after birth, and the total time that a female spends rearing a litter, from conception to weaning, totals approximately 80 days (Eisenberg 1981; O'Connell 1983). Considering the three-month breeding period of *M. incana* described above, and assuming a rearing cycle similar to that of *M. robinsoni*, a female could only produce a single litter within one reproductive season. This hypothesis is corroborated in our results by the restricted, consecutive and unrepeated occurrence of the female mammary stages for the total sample, aside from the Ilhéus exceptions (Fig. 2). Furthermore, the limited breeding season shown by *M. incana* is also an indication that the female estrous cycle is monoestric, or, at least, seasonally polyestric, in a very limited interval of time.

The above evidence suggests that in *Marmosa incana* each individual takes part in only one reproductive season except in the Ilhéus population, where, occasionally, two independent breeding seasons may occur within a year. Consequently, in localities where there is no additional reproductive season, *Marmosa incana* reproduces only once in a lifetime, which characterizes a semelparous way of life.

Rare among vertebrates, a semelparous strategy was originally demonstrated among mammals in the dasyurid marsupial *Antechinus stuartii*. This species presents a total turnover of the male cohort within consecutive generations owing to the death of all adult males after the reproductive period. A monestrous cycle in the female and a synchronous pattern of breeding within a short interval of time, in a local population, were also documented.

Braithwaite and Lee (1977) suggested that semelparity is the extreme expression of a strategy characterized by an intense and highly synchronized reproductive effort where

juvenile survival is consistently higher during one season of the year. Under this assumption, the development of semelparity in mammals would be favored among species showing a maximum field longevity of approximately one year and an annual optimal period for reproduction of sufficient duration for individuals females to raise successfully one but not two litters (Braithwaite and Lee 1977). These authors considered marsupials weighting less than 1 kg and living in predictable, highly seasonal environments to be the prime candidates for semelparity among mammals.

In keeping with these predictions, all presumptive examples of semelparous mammals suggested since then are small marsupials confined to highly seasonal habitats. Indeed, among New World mammals the only indication of semelparity was obtained in a restricted population of the didelphid marsupial *Monodelphis dimidiata* at Balcarce, Buenos Aires province, Argentina. In this locality none of the adult individuals survive to the first winter, or into the winter, after the reproductive period (Pine et al. 1985). It is noteworthy that records of *M. dimidiata* to the north of Balcarce did not corroborate the semelparous pattern.

Similar to *Monodelphis dimidiata, Marmosa incana* also shows a small body size (total weight is less than 120 g in males and 80 g in females). As revealed by the present study however, semelparity seems to be a rather widespread phenomenon in *Marmosa incana*. This species is best known from the humid Atlantic forests of eastern Brazil (Streilein 1982), a relatively constant environment, where temperatures do not show extreme variations in the course of the year. Although there is some seasonality in rainfall, especially in the Minas Gerais localities, this cannot be considered a predictable, strongly seasonal environment, as the habitats seem to be of all semelparous mammals reported to date. In the sample analysed, the semelparous pattern was corroborated in all localities except the Ilhéus sample, where it is not impossible that some females take part in more than one breeding period. Although seasonality may constitute an important condition for the evolution of semelparity in mammals, it appears, from our analysis, that this reproductive strategy may also exist in more constant environments than those previously hypothesized.

Acknowledgements

We are greateful to the curators of mammal collections at Museu Nacional (UFRJ), Departamento de Zoologia (UFMG), Museu de Biologia Mello Leitão, and Museu de História Natural "Capão da Imbuia", who kindly allowed us to study the specimens under their care. We express our gratitute to Drs. L. M. Pessôa and D. M. Teixeira for their help and use of facilities and critical revision of preliminary versions of this manuscript. We thank G. Reed for the revision of the English version and M. Pessôa for the drawings. Work by the authors was partially supported by graduate fellowships from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

Zusammenfassung

Jahreszeitliche Altersstruktur und Fortpflanzung bei Marmosa incana (Lund, 1841) (Didelphidae, Marsupialia)

Jahreszeitliche Altersstruktur und Fortpflanzungsanzeichen wurden bei 311 Sammlungsexemplaren des Mausopossums *Marmosa incana* studiert. Die monatlichen Häufigkeiten relativer Altersklassen, die nach Zahndurchbruch und -abnutzung festgelegt wurden, deuten auf einen fast vollständigen Wechsel der Population im Jahreslauf (1 Jahr bei Männchen, 1,5 Jahre bei Weibchen). Die Analyse des Fortpflanzungszustandes zeigte, daß alle sexuell aktiven Tiere in die beiden höchsten Altersklassen fallen. Diese Populationsmerkmale und eine im größten Teil des Verbreitungsareals von *Marmosa incana* festgestellte dreimonatige saisonale Fortpflanzungsperiode deuten auf einen ungewöhnlichen Lebenszyklus mit nur einmaliger Reproduktion hin.

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Authors' addresses: Maria Lucia Lorini and João A. de Oliveira, Seção de Mastozoologia, Museu Nacional (UFRJ), Quinta de Boa Vista, s/n°, CEP 20940-040. Rio de Janeiro, RJ, Brazil; Vanessa G. Persson, Museu de História Natural "Capão da Imbuia", Rua Prof. Benedito Conceição 407, CEP 82810-080, Curitiba, PR, Brazil

Z. Säugetierkunde 59 (1994) 74–81

ISSN 0044-3468

Food and feeding habits of insectivorous bats from Israel

By J. O. Whitaker, Jr., B. Shalmon, and T. H. Kunz

Department of Life Sciences, Indiana State University, Terre Haute, USA, Israel Mammal Information Center, Eilat Field School, Eilat, Israel, and Department of Biology, Boston University, Boston, USA

Receipt of Ms. 14. 5. 1993
Acceptance of Ms. 21. 9. 1993

Abstract

Small numbers of fecal pellets were examined from nine of the 32 species of insectivorous bats from Israel. Based on these small samples, *Asellia tridens* and *Pipistrellus bodenheimeri* were lepidopteran/dipteran and lepidopteran/dipteran/coleopteran feeders, respectively; *Myotis nattereri* fed primarily on lygaeids and coleopterans; *Otonycteris hemprichi* fed exclusively on coleopterans; *Pipistrellus kuhlii* fed on hymenopterans and coleopterans; *Pipistrellus rueppelli* and *Tadarida teniotis* fed mostly on lepidopterans and coleopterans; *Plecotus austriacus* fed exclusively on lepidopterans, and *Rhinolophus clivosus* was a generalist feeder, taking several different kinds of insect prey. Information on dietary analysis is supplemented with direct observations on the foraging habits of these bats.

Introduction

Knowledge of an animal's diet is important for interpreting its ecological role as a predator and its impact on local environments. Such knowledge is especially important as natural habitats are being altered owing to increased urbanization, modern agricultural practices (intense irrigation and pesticide applications), and deforestation. In recent years, the use of pesticides in Israel was rated second in the world per capita (Makin 1989). Thus, knowledge of their insect prey is important for assessing the potential value of bats in controlling insect pests, especially in areas where urban and cultivated lands have replaced natural habitats.

There have been a limited number of observations on food habits and foraging behavior of bats in Israel (Makin 1987; Bates and Harrison 1989; Harrison and Bates 1991; Yom-Tov 1993; Yom-Tov et al. 1992a, b), and only one substantial report on foraging behavior (*Pipistrellus kuhlii*, Barak and Yom-Tov 1989). Yom-Tov's (1993) analysis of morphological characters of insectivorous bats in the Dead Sea area is the most comprehensive account of foraging characteristics of bats in Israel. The purpose of this study is to present preliminary information on food and feeding habits on selected insectivorous bats in Israel, based primarily on samples of fecal remains collected from bats captured at feeding sites. These results are supplemented by observations of foraging behaviour at sites where bats were captured.

Material and methods

Fecal pellets were collected from nine species of bats, eight of which were captured in mist nets set at feeding sites. These include *Asellia tridens, Myotis nattereri, Pipistrellus bodenheimeri, Pipistrellus kuhlii, P. rueppelli, Plecotus austriacus, Otonycteris hemprichi, Rhinolophus clivosus,* and *Tadarida teniotis* (feces from the latter species was collected at a roosting site). Following capture, individuals of each species were placed in holding bags allowing feces to be deposited before releasing the bats at the site of capture. Collection localities for each species are noted below. Most collection sites were located in the vicinity of the Dead Sea. A summary of the geography, climate, and vegetation in this region is given in Yom-Tov et al. (1992b).

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We used fecal analysis to assess food habits so we could release the bats alive after collecting the feces for analysis. For insectivorous bats, this method is comparable to stomach content analysis (KUNZ and WHITAKER 1983). Contents of fecal samples were identified to family and analyzed using the methods described in WHITAKER (1988). Each pellet was examined separately and the percent volume of each food item was estimated visually in each pellet. Most results are presented as overall percent volume (sum of individual volumes/total volume for the sample × 100) and percent frequency (number of pellets of occurrence/total number of pellets in sample × 100). Observations of feeding behavior were made at the time bats were captured and fortuitously at other times. These were supplemented by unpublished observations and those reported by YOM-TOV et al. (1992a, b). Unless otherwise noted, means and standard deviations for body masses of bats are from YOM-TOV et al. (1992b).

Results and discussion

Data on nine species of insectivorous bats known from Israel are summarized below.

Asellia tridens (12 pellets, 2–5 mm long, $\bar{x}$ = 4.9 mm, from Navit Pools). This bat ranges across northern Africa from Morocco and Senegal to Egypt and Ethiopia, Zanzibar, Arabian Peninsula to Pakistan. In Israel bats were captured over a fresh water pool surrounded by lush vegetation at an oasis south of the Dead Sea. All contained Lepidoptera (61,3 % volume, 100 % frequency) and all but one contained Diptera, mostly chironomids (38.8 % volume, 91.7 % frequency). Based on an analysis of 147 fecal pellets from this bat collected at an abandoned mine (North of Elat), the following prey items (expressed as percent frequency) were taken: Coleoptera (59), Hymenoptera (21), Orthoptera (14), Lepidoptera (3), Diptera (2), and Odonata (1).

This medium sized bat ($\bar{x}$ = 9.8 g ± 1.9 g) is known to take large insects (Tettigoniidae, Blattodea, and Lepidoptera) and transport them to underground shelters where they are consumed. The diet of *A. tridens*, as determined in the present study, is consistent with its habit of foraging over bodies of water and its use of Doppler-shift compensation (GUSTAFSON and SCHNITZLER 1979), which may allow it to use information on the wing-beat frequency of certain insects to facilitate prey capture. The echolocating calls have the highest recorded frequency (around 121 kHz) among the bats in Israel. One of us (B. SHALMON) observed *A. tridens* flying around street lights in the settlements of Hazeva and En Gedi. This bat reportedly is nearly extinct in the Mediterranean zone in Israel, and is confined mostly to drier zones (MAKIN 1989). This bat is a highly desert-adapted species that reportedly roosts (and feeds) in the vicinity of oases (GAISLER et al. 1972). In Oman it has been observed flying near the ground and feeding in palm groves (NOWAK 1991).

Myotis nattereri (2 pellets, both 4 mm long, from Zoarim Cave, Upper Galilee). This 9–11 g bat is a widespread species, ranging from northern Europe southward to Morocco, across central Asia to Japan. In Israel, individuals were captured in dense Mediterranean maquis, where it was also observed feeding. Four prey items were identified with percent volumes and frequencies as follows: Lygaeidae (42.5 %, 50 %), Coleoptera (42.5 %, 100 %), spider (10 %, 50 %) and Diptera (5 %, 50 %).

Compared with similar species of *Myotis* (e.g. *M. capaccinii*), the intensity of echolocation calls is very low. It has morphological adaptations for slow, maneuverable flight (NORBERG and RAYNER 1987); in Scandinavia this bat feeds along the contours of trees, often among the branches (BAAGØE 1987). The relatively wide diversity of prey taken, including Diptera, suggests that it also feeds near water.

Otonycris hemprichi (11 pellets, 3–7 mm, $\bar{x}$ = 5.0, from Sapir). Bats were captured over a fresh water pool in arid habitat, surrounded by vegetation. All fecal pellets examined contained 100 % Scarabaeidae. This relatively large ($\bar{x}$ = 19.0 g ± 2.0 g) long-eared, desert-dwelling bat ranges from the arid regions of Morocco and northern Niger through Egypt and across the northern Arabian Peninsula to Kazakhastan and Pakistan (NOWAK 1991; HARRISON and BATES 1991). This bat flutters like a large butterfly over water and nearby vegetation (YOM-TOV 1993). In southern Kirghizia (central Asia) this bat has been

observed foraging close to rock surfaces (Rybin et al. 1989). Typical of gleaners, *O. hemprichi* is a low-intensity echolocating or whispering bat. At times it probably relies on vision and passive listening to locate its prey. Based on an analysis of its body mass and wing morphology (low aspect ratio and low wing loading), Fenton and Norberg (1988) postulated this bat should be carnivorous. In Israel it has been captured while foraging in a date palm grove and, in nearby Jordan, it has been captured over a small pool in an arid mountain gorge (Bates and Harrison 1989).

Pipistrellus bodenheimeri (14 pellets 2–4 mm long, $\bar{x}$ = 2.8). Fourteen pellets were examined from three different localities (Tab. 1). Overall, the most important food items included Lepidoptera, Coleoptera, and Diptera. Lepidopterans were the major food at two localities followed by chrysomelid beetles at one and dipterans at the other. Dipterans were the principal food item followed by coleopterans at the third locality. This small bat ($\bar{x}$ = 2.7 g ± 0.2 g) is restricted to extreme desert areas in Israel, the Sinai Peninsula and the southwestern Arabian Peninsula (Nowak 1991; Yom-Tov 1993). It appears to be an opportunistic predator, although lepidopterans comprised most of its diet in our sample. It was collected in open desert habitats, around street lamps in the settlements of Elat, En Gedi, and over freshwater pools in nearby arid regions. Although this bat may hibernate from October through April in Israel, it has been observed feeding in all months of the year (Yom-Tov et al. 1992a). In winter, the number of bats feeding near street lights is considerably smaller than during the summer months. In the Arabian peninsula, this bat has been observed flying (foraging?) along rows of tamarisk and eucalyptus trees that were planted around a cultivated area surrounded by desert and acacia trees (Harrison and Bates 1991).

Table 1. **Food as indicated by 14 fecal pellets from *Pipistrellus bodenheimeri* at three localities in Israel**

	Sapir 18. 5. 1988		En Gedi 3. 3. 1988 25. 4. 1988		Neot Hakikar 3. 7. 1989	
Number of Pellets	5		7		2	
	% vol.	% freq.	% vol.	% freq.	% vol.	% freq.
Lepidoptera	71.0	100	68.6	100	—	—
Chrysomelidae	19.0	100	—	—	—	—
Scarabaeidae	4.0	40	—	—	—	—
Insect	3.0	40	—	—	—	—
Coleoptera	1.6	20	—	—	37.5	50.0
Chironomidae	1.4	40	—	—	—	—
Diptera	—	—	30	100	62.5	100
Spider	—	—	1.4	14.2	—	—

Pipistrellus kuhlii (5 pellets 2–5 mm, $\bar{x}$ = 3.4, from Upper Galilee). Parts of winged ants (alates) were the most important items collected from individuals captured near street lamps at Sasa (56 % volume, 100 % frequency), followed by Coleoptera (24 %, 60 %), Chrysomelidae (8 %, 20 %) Lepidoptera (6 %, 60 %), Cerambycidae (4 %, 20 %) and unidentified insect remains (2 %, 20 %). One of the most common bats in Israel, this small, $\bar{x}$ = 7.0 g ± 0.5 g, species is known from southern Europe, southwestern Asia, northern, eastern, and southern Africa, and the Canary Islands (Kingdon 1974; Nowak 1991). Its feeding activity occurs mostly within the first three hours following sunset and is characterized by low, fast feeding flights in open areas. In urban areas it feeds on flying insects attracted to street lights (Haffner and Stutz 1985–86) and over water (Vernier 1989). In east Africa, Kingdon (1974) noted that this bat was attracted to insects swarming around ripe fruits on a peach tree. Schnitzler et al. (1987) indicated that it relies on low

frequency echolocation calls (35–40 kHz), which is typical of bats feeding in open areas (NEUWEILER 1983).

BARAK and YOM-TOV (1989) suggested that the echolocation calls produced by *P. kuhlii* caused some of the flying insects attracted to street lights (none were identified) to disperse and thus improve an individual bat's ability to capture prey. Evidence for this hypothesis was based on the observation that feeding rates were highest at those sites whee foraging group size increased from one to five individuals. Feeding rates of individual bats were lower when fewer bats were present, suggesting that prey capture in *P. kuhlii* is enhanced by feeding in small groups.

Pipistrellus rueppelli (7 pellets 2–7 mm, $\bar{x}$ = 3.3, from Navit Pools). Six of seven pellets examined contained 100 % lepidopterans. The seventh contained 65 % Lepidoptera and 35 % (volume) unidentified material. This 7.0 g ± 0.5 g Afrotropical species ranges from Egypt to Senegal and south to Angola and Botswana (HARRISON and BATES 1991), and southern Iraq (YOM-TOV et al. 1992b). In Israel this bat was captured while flying over small freshwater pools. In East Africa, it is known from savannah and arid regions, where it has been observed flying (feeding?) along rivers at dusk (KINGDON 1974; SKINNER and SMITHERS 1990). LANG and CHAPIN (1917) reported *P. rueppelli* flying (feeding?) adjacent to oil palms in riparian habitat. SKINNER and SMITHERS (1990) noted that *P. rueppelli* is also associated with rivers and swamps.

Plecotus austriacus (5 pellets 3–6 mm, $\bar{x}$ = 4.0, from Sapir). Bats with long ears (e.g., *Plecotus* and some other genera) are often lepidopteran specialists (FENTON and NORBERG 1988). Judging from our findings, *P. austriacus* is indeed a lepidopteran specialist, as all pellets examined contained 100 % Lepidoptera. This low-intensity echolocating bat ($\bar{x}$ = 6.7 ± 1.1 g) is known from southern Europe and Northern Africa, westward to Mongolia and western China, Cape Verde Islands and Senegal (NOWAK 1991). As with other members of its genus, *P. austriacus* is known to hover and glean insects from vegetation and other surfaces (ROBERTS 1977). Its short, broad wings, and low flight speed (NORBERG and RAYNER 1987) presumably facilitate captures of resting insects in these situations. Judging from its small size and weak dentition, ROBERTS (1977) suggested that this bat probably feeds "mainly on smaller moths, spiders and lacewings (*Planipennia* sp.)".

Rhinolophus clivosus (5 pellets 2–7 mm, $\bar{x}$ = 4.2, from En Gedi). Even though the available fecal sample was extremely small, six separate prey items were taken: Coleoptera, probably Chrysomelidae (53 %, 80 %); Hymenoptera (31 %, 20 %); Lepidoptera (11 %, 80 %); Insect (2 %, 40 %); Scarabaeidae (2 %, 20 %) and Lygaeidae (1 %, 20 %). This medium size bat ($\bar{x}$ = 11.0 g ± 2.0 g) is known from central and southwestern Asia, and in Africa from Liberia and Algeria eastward to Cameroon (NOWAK 1991), and southward to Southern Africa (HARRISON and BATES 1991; SKINNER and SMITHERS 1990). When foraging it flies below tree-top level (RAUTENBACH 1982) and low around trees and shrubs. In Israel, individuals were captured as they flew low between trees in the desert oasis of En Gedi. Elsewhere, the food items taken by this bat includes moths and small beetles (SKINNER and *Smithers* 1990), although it sometimes eats large beetles (KINGDON 1990). This bat establishes feeding roosts on branches of trees and beneath verandahs of houses where individuals cull hard parts of insects before eating them (RAUTENBACH 1982).

Tadarida teniotis. Nine samples were available, all from Karmiel (Lower Galilee). Fifty pellets were selected from each of these samples. Pellets were selected in order to include all sizes, from largest to smallest. Pellets ranged from 3 to 10 mm long, but averaged about 6 to 7 mm. Prey items as indicated by these nine samples are shown in table 2. Lepidopterans were the most important food, ranging from 65.4 % to 87.6 % by volume of the total material examined. Of the 450 pellets examined, 442 or 98.2 % of them contained moths, whereas 215 of these pellets or 47.8 % contained 100 % of this material. Coleopterans, especially ground beetles (Carabidae) and June beetles (Scarabaeidae), were the second most important food items. The amount of beetles eaten ranged from 6.8 % to 27.3 %

Table 2. **Food of *Tadarida teniotis* (% volume) on Karmiel, Israel, as indicated by nine samples of 50 pellets each on 9 different dates**

Dates	17. 8. 1991	3. 9. 1991	15. 3. 1992	15.–16. 3. 1992	16.–17. 3. 1992	18. 3. 1992	23. 6. 1992	25. 7. 1992	25.–26. 7. 1992
LEPIDOPTERA	75.5	76.3	82.4	69.6	65.4	87.0	75.3	85.4	87.6
COLEOPTERA[1]	(21.5)	(17.6)	(15.6)	(27.3)	(22.9)	(6.8)	(12.1)	(11.2)	(7.2)
Scarabaeidae	8.7	8.0	2.0	15.4	11.6	4.9	2.4	3.8	1.8
Carabidae	7.5	5.9	9.7	8.3	9.0	0.2	7.8	2.7	0.8
Tenebrionidae	—	1.7	—	—	—	—	—	—	—
Chrysomelidae	4.2	0.5	3.2	0.3	0.2	—	—	0.1	1.7
Curculionidae	—	0.2	—	—	—	—	0.4	0.6	0.3
Unid. Coleoptera	1.1	1.3	0.7	3.3	2.1	1.7	1.5	4.0	2.6
HEMIPTERA/HOMOPTERA									
Lygaiedae	1.4	1.1	2.0	1.4	4.6	1.8	4.2	0.9	1.4
Cicadellidae	—	0.3	—	—	—	—	1.1	—	—
Green Pentatomid	—	—	—	—	0.3	—	—	0.5	—
Unid. Hemiptera	—	—	—	1.5	—	—	—	—	—
ORTHOPTERA									
Gyllidae	1.2	1.5	—	0.2	6.8	4.3	7.3	1.8	3.8
HYMENOPTERA									
FORMICIDAE	—	0.3	—	—	—	—	—	—	—
DIPTERA	0.3	0.2	—	—	—	—	—	0.1	—
NEUROPTERA									
Hemerobiidae	—	0.1	—	—	—	—	—	—	—
EPHEMERIDA	—	1.3	—	—	—	—	—	—	—
Unidentified Insect	—	1.4	—	0.1	—	—	—	—	—
ACARINA (mites)	0.02	—	—	—	—	—	—	—	—

[1]Total Coleoptera volumes are given in parentheses.

volume. Crickets (Orthoptera: Gryllidae) also were regularly eaten, with consumption ranging upwards to 7.3 % volume.

This relatively large insectivorous bat ($\bar{x}$ = 18.5 ± 2.0 g) has a wide distribution, ranging from Madeira, the Canary Islands, Morocco and the Iberian peninsula, eastwards through North Africa and southern Europe to southern China, Tiawan and Japan (HARRISON and BATES 1991). *Tadarida teniotis* is a fast, high flying bat (GAISLER and KOWALSKI 1986) often observed 20–50 m above the ground where it feeds largely on moths. In Israel it is commonly observed flying above settlements and cities, feeding on such insects attracted to street lights. The high intensity, low frequency (12–14 kHz) echolocation calls of this bat are audible to humans. It is one of the most beneficial bats to farmers, which suffer heavy damage to crops from noctuid moths (e.g., *Spodoptera litoralis, Argotis ipsilon*, and *Earias insulana*). Other reports indicated that members of the genus *Tadarida* are often generalist feeders, but consume large numbers of moths (e.g., ROSS 1967; KUNZ et al. 1994).

Based on our preliminary dietary analysis of nine species of insectivorous bats from Israel, some appear to specialize either on coleopterans (beetles) or on lepidopterans (moths), whereas others are generalist predators. As in other species of insectivorous bats, food habits can be expeced to vary depending on the locality, season, and ability of the bat to detect (visually or accoustically) certain types of insects, and morphological characteristics. Using an analysis of morphological characteristics, YOM-TOV (1993) placed 15 species of bats known from the Dead Sea area into three feeding guilds as follows: Guild 1 included species with long wing tips, third digits and articulating metacarpals 1.3 times, or more, longer than the forearm, and normal-size ears (forearm/ear ratio was 2.5 or larger). Species in the present study that were included in YOM-TOV's guild 1 include *Asellia tridens, Rhinolophus clivosus, Pipistrellus bodenheimeri, P. rueppelli, P. kuhlii*, and *Tadarida teniotis*. These bats feed in a variety of habitats, including high altitudes (*Tadarida*) at medium to low heights (*Pipistrellus*), or forage amongst vegetation (*Asellia, Rhinolophus*). YOM-TOV's guild 2 included species with wing tips that are similar to species listed in Guild 1, but each have exceptionally large ears (exceeding 30 mm), which are twice the size of other bats included in his analysis. The two species which YOM-TOV included in Guild 2, and that we also examined, include *Otonyceris hemprichi* and *Plecotus austriacus*. Both species fly low and slowly and produce low-intensity echolocation calls (i.e., whispering bats). None of the species listed in YOM-TOV's guild 3 were included in our study. Although morphological data may offer general insights into the feeding ecology of an animal (e.g., FREEMAN 1988; FENTON and NORBERG 1988; YOM-TOV 1993), it cannot be used to predict the behavioral or dietary variability such as we observed in the present study.

Acknowledgements

We wish to thank D. FRANKO (Karmiel) for collecting fecal samples of *Tadarida teniotis* and Y. MOSKIN for sharing observations on echolocation-call characteristics and feeding habits of *Myotis nattereri*. Y. YOM-TOV (Tel Aviv University) kindly commented on an earlier draft of this manuscript. This project was facilitated by a travel grant from the Conanima Foundation to THK.

Zusammenfassung

Nahrung und Ernährungsverhalten einiger insektivorer Fledermäuse aus Israel

Kleine Proben von Kotpillen von 9 der 32 in Israel vorkommenden insektivoren Fledermausarten wurden analysiert. Nach diesen Proben fraß *Asellia tridens* (n = 12) überwiegend Lepidoptera, Diptera und Coleoptera. *Myotis nattereri* ernährte sich vorwiegend von Lygaeidae und Coleoptera; *Otonycteris hemprichi* ausschließlich von Coleoptera; *Pipistrellus kuhlii* von Hymenoptera und Coleoptera; *Pipistrellus rueppelli* und *Tadarida teniotis* überwiegend von Lepidoptera und Coleoptera; *Plecotus austriacus* ausschließlich von Lepidoptera, und *Rhinolophus clivosus* erwies sich als Generalist

und nahm viele verschiedene Insekten als Nahrung. Ergänzend werden Direktbeobachtungen über das Suchverhalten dieser Fledermäuse mitgeteilt.

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Authors' addresses: Prof. J. O. WHITAKER, Jr., Department of Life Sciences, Indiana State University, Terre Haute, Indiana 47809, USA; Dr. B. SHALMON, Israel Mammal Information Center, Eilat Field School, Eilat, 88101, Israel, and Prof. T. H. KUNZ, Department of Biology, Boston University, Boston, MA 02215, USA

Z. Säugetierkunde 59 (1994) 82–86

ISSN 0044-3468

Seasonal food habits of coyotes, *Canis latrans*, in the Bolsón de Mapimí, Southern Chihuahuan Desert, Mexico

By LUCINA HERNÁNDEZ and M. DELIBES

Instituto de Ecología, Durango, Mexico and Estación Biológica de Doñana, Sevilla, España

Receipt of Ms. 01. 03. 1993
Acceptance of Ms. 16. 09. 1993

Abstract

Studied the seasonal foods of coyotes, *Canis latrans*, at the Biosphere Reserve of Mapimí in the Southern Chihuahuan Desert, Mexico, by analysis of 508 faeces (scats) collected between March 1985 and November 1986. Lagomorphs were the most frequent food, occurring in 49 % of the samples, followed by fruits (33 %) and rodents (32 %). There were important seasonal and interannual changes in food habits. As a rule, lagomorphs were the most frequent item in autumn and winter, but fruits (mainly *Opuntia* sp.) predominated in summer and rodents (mainly *Neotoma albigula*) in spring. Birds and reptiles were consumed to a low proportion and ungulates were eaten only when carcasses were available. Our data suggest that the coyoe in this area behaves as a selective predator of rabbits, occasionally using abundant alternative foods in an opportunistic way.

Introduction

The ecology of coyotes *Canis latrans* is among the best known of all carnivores (BEKOFF 1982). However, most investigations have been carried on in the United States and Canada. Thus, information about the food habits of coyotes in the southern region of its range is rather scarce. Studies on coyotes' diet in Mexico have been conducted at cattle ranches of Chihuahua, where the main food was carrion (PÉREZ GUTIÉRREZ et al. 1982) and vegetables (VELA 1985), and in pineoak forests of the Sierra Madre Occidental, where the spring-summer staple prey were rodents, arthropods and berries (DELIBES et al. 1989). In addition, most ecological research on coyotes has been conducted in agricultural regions, where this species is usually considered as a pest (VOIGT and BERG 1987). Thus, studies in desert areas are lacking. In a previous investigation, HERNÁNDEZ et al. (1993) reported on the autumn food habits of coyotes in some areas of the deserts of Sonora and Chihuahua. The aim of this study is to report on seasonal food habits of this species in the Mapimí Biosphere Reserve of the Southern Chihuahuan desert.

Study area

The study was made in the surroundings of the field laboratory of the Mapimí Biosphere Reserve, located in the Mapimí Bolsón area, close to the vertex formed by the Mexican states of Chihuahua, Coahuila and Durango (ca. 26°40′ N, 103°45′ W). The area is a flat plain (average altitude 1100 m above sea level) with poor drainage. Vegetation is low and scattered, dominated by creosote bush (*Larrea tridentata*), mesquite (*Prosopis glandulosa*), prickly-pear (*Opuntia* sp.) and agave (*Agave* sp.). A recent vegetation map of the area has been published by MONTAÑA (1988). Climate is semiarid, with irregular summer rains (263 mm per year on average) and mean monthly temperatures ranging from 12 °C in January to 28 °C in June and July (CORNET 1988).

Material and methods

By walking along a stretch of dirt roads of approximately 10 km in the reserve every month, from March 1985 to November 1986, we collected a total of 508 coyote faeces. Faeces (scats) were identified by size, scent and the nearby presence of coyote tracks. We used hairs, teeth, bones, feathers, scales, any other hard structures, and seeds to identify prey species by comparison with a reference collection. We were unable to differentiate the remains of black-tailed jackrabbits (*Lepus californicus*) from those of desert cottontails (*Sylvilagus auduboni*). Number of occurrences and percent frequency of occurrence (number of occurrences × 100/number of scats) were obtained for each food species or group. These data did not accurately reflect the weight of ingested material, but they are usually considered to yield a good representation of food habits (e.g., NIEBAUER and RONGSTAD 1977).

Monthly samples were grouped into four seasons: spring (March to May), summer (June to August), autumn (September to November), and winter (December to January). Seasonal differences in the occurrence of particular items were determined by contingency-table analysis (G-test) (SOKAL and ROHLF 1981).

Results

Lagomorphs were the most frequently occurring food item, followed by fruit and rodents. Ungulates, birds, reptiles, arthropods and garbage (plastic material) were only rarely ingested (Tab. 1).

By pooling data corresponding to seasons from 1985 and 1986, it was found that lagomorphs were the most frequent item in autumn (45.3 % of occurrences) and winter (57.3 %), while they occupied a second place in spring (34.1 %) and summer (28.5 %). However, interannual differences were significant (Table). Seasonal frequency of occurrence of lagomorphs was not related to estimations of lagomorph abundance in the field.

Fruits were the most frequent item in the scats collected in summer (50.3 % of occurrences), but ranged on third place in spring (18.4 %), autumn (16.1 %), and winter (12.9 %). Prickly-pear was the most commonly consumed fruit, followed by mesquite. Both were eaten in high proportions in summer, when they were ripe. Turk head (*Hamatocactus hamattocanthus*) fruit was consumed in winter, while lotebush (*Ziziphus obtusifolia*) was frequent in summer (1985) and spring (1986) (the fructification of this shrub shows a considerable plasticity in response to autumn precipitation; FOSTER et al. 1984). Althorn (*Castella texana*) fruit was consumed during the first spring.

Rodents were the most frequent item in the scats collected in spring (35.7 %), and they occupied a second place in autumn (32.8 %) as well as in winter (21 %), and the third place in summer (13.5 %). Woodrats (*Neotoma albigula*) were the most commonly consumed rodents, especially in spring (1985), followed by kangaroo rats (*Dipodomys* sp.), deer mice (*Peromyscus* sp.) and pocket mice (*Perognathus* sp.). Ground squirrels (*Spermophilus spilosoma* and *Spermophilus mexicana*) primarily appeared during the first autumn.

Birds and reptiles were consumed to a low proportion, and there were no seasonal trends in their utilization (Table). Arthropods (mainly beetles and grasshoppers) were consumed especially in spring and summer. Carcasses of calves were eaten during the second spring, when there was a high mortality of cattle caused by disease. Remains of mule deer (*Odocoileus hemionus*) appeared in the faeces mainly in winter, at the same time when we observed some coyotes feeding upon two carcasses of deer killed by mountain lions (*Felis concolor*).

Discussion

Our data suggest that lagomorphs were the staple prey for coyotes in Mapimí, as it occurs in other areas (SHORT 1979). Nevertheless, a seasonally high availability of alternative prey (mainly prickly-pears in summer) will produce a change to these temporally abundant foods, even when leporids are present at a high level of population size (e.g., in summer 1986). As found by other authors (MURIE 1945; JOHNSON and HANSEN 1977, 1979), it

Occurrences of different foods in the faeces of coyotes

Season N	SP85 (68)	SM85 (77)	AT85 (64)	WT85 (101)	SP86 (75)	SM86 (70)	AT86 (53)	Total (508)	FO	G Values
Ungulates										
Bos taurus	1	0	2	0	6	0	0	9	1.7	19.4**
Odocoileus hemionus	0	1	0	4	0	0	0	5	0.9	11.7 ns
Lagomorphs	34	36	29	71	29	19	33	251	49.4	24.2***
Rodents										
Neotoma albigula	18	13	5	14	13	3	11	77	15.1	16.5*
Dipodomys sp.	8	2	7	9	11	4	3	44	8.6	9.8 ns
Spermophilus sp.	0	0	4	1	1	0	0	6	1.1	13.5*
Perognathus sp.	3	1	2	2	0	0	6	14	2.7	18.7**
Peromyscus sp.	1	0	6	0	8	0	0	15	2.9	32.6***
Unidentified	2	3	0	0	1	0	1	7	1.3	9.4 ns
Birds	1	0	1	4	4	1	2	13	2.5	7.8 ns
Reptiles	3	0	1	0	1	2	1	8	1.5	8.8 ns
Arthropods	4	2	0	1	2	9	0	18	3.5	21.9**
Fruit										
Prosopis glandulosa	0	7	4	2	1	10	0	24	4.7	26.8***
Opuntia sp.	0	30	10	2	6	34	4	86	16.9	92.3***
Hamatocactus hamattocanthus	1	0	0	9	1	0	0	11	2.1	24.0***
Ziziphus obtusifolia	3	8	0	0	10	2	0	23	4.5	30.3***
Castella texana	4	1	1	0	0	0	0	6	1.1	13.6*
Castella texana	1	1	3	3	7	4	0	19	3.7	11.5 ns
Other vegetables	0	0	1	2	0	0	0	3	0.5	6.9 ns

SP = Spring; SM = Summer; AT = Autum; WT = Winter; 85 = year 1985; 86 = year 1986; N = Number of faeces analysed in each season; FO = total frequency of occurrence (number of occurrences of each item × 100 number of faeces). G test indicates differences between periods in the proportion of prey consumed. *** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; ns = not significant.

appears that coyotes seek lagomorphs or some other abundant food and make it their basic prey throughout the year. This fact suggests that they are selective rather than opportunistic feeders. The high occurrence of leporids in the diet during the winter of 1985, when being relatively scarce in the study area, supports this statement. Conversely, changes in the abundance of alternative prey were paralelled by seasonal variations in the frequency of occurrence of these foods in samples, as noted for rodents in a similar area in Texas (WINDBERG 1985). This foraging behaviour (a selective predator occasionally using abundant alternative foods in an opportunistic way) is similar to that reported for the European badger (*Meles meles*) by KRUUK and PARISH (1981).

Prickly-pears and woodrats were important buffer prey for coyotes in Mapimi. We found that two radiotracked coyotes in the area showed a strong preference for a structurally heterogeneous habitat with dominance of mesquite, creosote bush, galleta grass (*Hilaria mutica*) and prickly-pear, where woodrats (feeding on prickly-pears) were especially abundant (GRENOT and SERRANO 1981). This habitat type is relatively rare in the Reserve, but it seems to be preferred by coyotes, probably because of the abundance of these foods.

Our results differ from those of PEREZ-GUTIERREZ et al. (1982) probably due to the high cattle raising activity in their study areas. They found carrion as the main food item for coyotes, followed by lagomorphs and rodents. VELA (1985) obtained results similar to the present data in one of three areas that she studied, vegetables being the main item (followed by lagomorphs) in the other two.

In conclusion, lagomorphs are an important food for coyotes in the arid zones of north-central Mexico, their relative role in the diet changing according to the abundance of buffer foods. In areas such as the Mapimí Biosphere Reserve, where exploitation is very low, lagomorphs are the basic prey of coyotes, and changes in the density of this predator can probably be expected to follow changes in leporid abundance (CLARK 1972; TODD et al. 1981). The effects of coyotes on large wild and domestic ungulates in these areas seem to be scarce, their consumption being probably related to cattle diseases and mountain lion predation on deer.

Acknowledgements

This research was supported by the Instituto de Ecologia within the project "Mapimí" and by an agreement between the Mexican CONACYT and the Spanish CSIC. We gratefully acknowledge the field assistance of A. L. HERRERA, A. HERRERA and F. HERRERA. R. RUIZ DE ESPARZA helped in the identification of seeds and F. PIZARRO in the preparation of hair slides. Dr. E. EZCURRA provided helpful suggestions for improvement of the manuscript. N. BUSTAMANTE revised the English and C. KELLER prepared the German summary.

Zusammenfassung

Jahreszeitliche Ernährungsgewohnheiten von Kojoten, Canis latrans, im Bolsón- de Mapimí-Reservat, südliche Chihuahua-Wüste, Mexiko

Die Ernährung von Kojoten, *Canis latrans*, wurde im Biosphäre-Reservat Mapimí in der südlichen Chihuahua-Wüste untersucht anhand der Analyse von 508 Kotproben, die zwischen März 1985 und November 1986 monatlich eingesammelt wurden. Lagomorpha kamen häufiger vor und wurden in 49 % der Proben gefunden. Es folgten Früchte (33 %) und Nagetiere (32 %). Wichtige intra- und interannuale Änderungen in den Ernährungsgewohnheiten wurden festgestellt. Normalerweise stellten Lagomorpha den Hauptanteil der Nahrung im Herbst und Winter, während Früchte (hauptsächlich *Opuntia* sp.) im Sommer, und Nagetiere (vorwiegend *Neotoma albigula*) im Frühling gefressen wurden. Vögel und Reptilien bildeten nur einen geringen Anteil der Nahrung, und Ungulaten wurden nur als Aas gefressen. Unsere Daten lassen vermuten, daß Kojoten in diesem Gebiet eine selektive Bevorzugung von Kaninchen zeigen, sich aber auch in opportunistischer Weise von zahlreichen anderen Tieren und Pflanzen ernähren.

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Authors' addresses: LUCINA HERNÁNDEZ, Instituto de Ecología, Apdo. Postal 632, 34000-Durango, Dgo., México, and MIGUEL DELIBES, Estación Biológica de Doñana, CSIC, Apdo. 1056, E-41080 Sevilla, Spain

Z. Säugetierkunde 59 (1994) 87–104

ISSN 0044-3468

Hyoid structure, laryngeal anatomy, and vocalization in felids (Mammalia: Carnivora: Felidae)

By G. Peters and M. H. Hast

Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn, Germany, and Northwestern University Medical School, Chicago, USA

Receipt of Ms. 8. 3. 1993
Acceptance of Ms. 17. 9. 1993

Abstract

Two types of hyoid structure are found in the Felidae. In five species it contains a cartilaginous ligament, in all other species it is completely ossified. Traditionally, it has been hypothesized that the presence or absence of roaring and purring in the acoustic repertoires of Felidae is correlated with these differences in the structure of the hyoid. This character complex has been used as a major criterion in the systematics of the Felidae. The present study brings together all currently available data to test this hypothesis, and discusses new findings on laryngeal anatomy with respect to vocalization and the hyoidean apparatus in the family Felidae.

In the Felidae an incompletely ossified hyoid does not automatically cause a species' ability to roar as this vocalization is restricted to only three of the five species with this hyoid type. All felid species which have been proven to purr have a completely ossified hyoid, but definitive evidence of this vocalization is still lacking in many species with this type of hyoid. Therefore, it is not possible at present to decide whether a fully ossified hyoid automatically causes a species' ability to purr. A further type of vocalization is restricted to those four felid species with a vocal fold morphology differing from that of all other species of the family.

Introduction

Richard Owen (1834) was the first to hypothesize a correlation between hyoid structure (see Figs. 1–3) and the occurrence of the specific type of vocalization called roaring in certain species of the Felidae. Based on the differences he found in the structure of the hyoid between the lion (*Panthera leo*) (felid taxonomy used in this publication follows Honacki et al. [1982], unless otherwise stated) on the one hand, and other species investigated (cheetah-*Acinonyx jubatus*, caracal-*Lynx caracal,* flat-headed cat-*Felis planiceps,* and domestic cat-*F. silvestris* f. *catus*) on the other, he pointed out (p. 129) that for the lion:

"The larynx is consequently situated at a considerable distance from the posterior margin of the bony palate; but the soft palate is prolonged backwards to opposite the aperture of the glottis, and the tongue is proportinately increased in length. Thus a gradually expanding passage leads from the glottis, where the air is rendered sonorous, to the mouth, and it is not unlikely that the strong transverse ridges upon the bony palate may contribute, with the preceding trumpet-like structure, to give that intonation which is so aptly denominated 'the roar of the lion'."

Then, in discussing his findings on hyoid structure in the other felids studied, he stated, "From the difference in the voice, the feline animals might have been expected, à priori, to present some differences in that part of their anatomy which relates to it."

Pocock's (1916) comprehensive survey of the hyoidean apparatus in the Felidae was based on dissections of 23 species, extending the number of species studied to 24 of the 37 recent Felidae. Pocock confirmed Owen's morphological findings and also adopted his interpretation of the correlation between hyoid structure and the occurrence of roaring in

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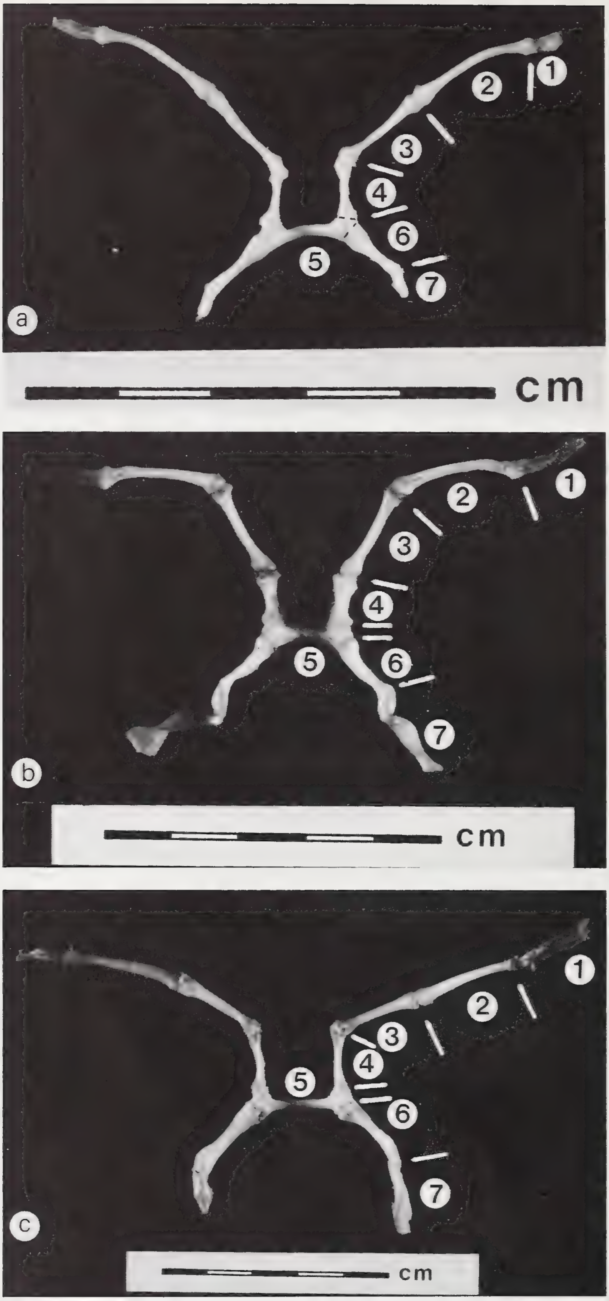

Fig. 1. The hyoid apparatus consists of a paired chain of bony/cartilaginous elements, connected by a single median element, the body of the hyoid. Both chains consist of a cranial and a caudal cornu each. Dorsal view of fully ossified hyoid apparatus of felid species a: domestic cat hybrid *(Felis s. silvestris × F. s.* f. catus) ad. ♀ (ZFMK 85.50), b: jungle cat (*Felis chaus*) ad. (ZFMK 86.123), and c: cheetah (*Acinonyx jubatus*) ad. ♀ (ZFMK 86.119). Scale 5 cm. Labeled structures (unilaterally only): 1 = tympanohyoid (cartilage); bones: 2 = stylohyoid; 3 = ephihyoid; 4 = ceratohyoid; 5 = basihyoid; 6 = thyrohyoid; 7 = chondrohyoid (cartilage). 1–4 = cranial cornu, 5 = body, 6 and 7 = caudal cornu of hyoid. (In a the border between body and the two cornua is marked on the bones for better visibility)

felids. According to Pocock, those species producing a roar are lion, leopard (*Panthera pardus*), jaguar (*P. onca*), and tiger (*P. tigris*); and in these the hyoid apparatus is not completely ossified (cf. Fig. 3). The snow leopard (*P. uncia*) is the only other felid species sharing this anatomical character, but its voice was not known to Pocock. All remaining species of this family very likely have a fully ossified hyoid (cf. Figs. 1, 2).

Pocock originally stated that the tympanohyal "... generally, if not always, remains cartilaginous through life up to its point of attachment with the bulla." (Pocock 1916: 222). However, recent textbooks on domestic cat anatomy like Crouch (1969) or Field and Taylor (1969) consider it to be a bone, or to consist of tight connective tissue (Nickel

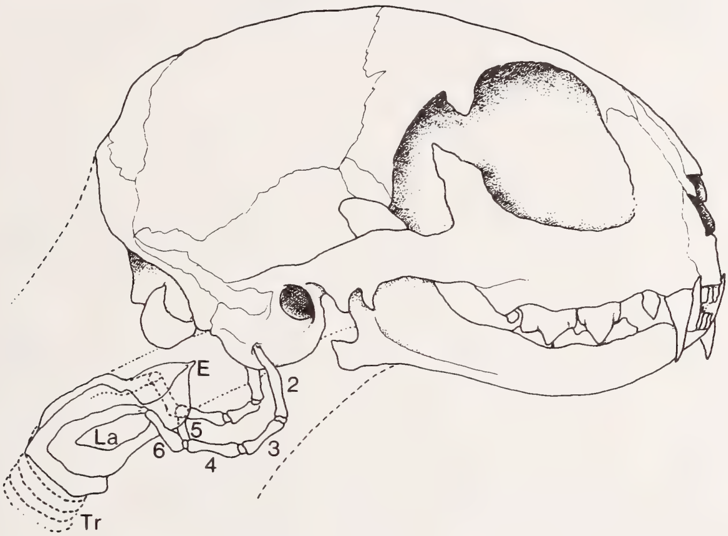

Fig. 2. Attachment of hyoid apparatus to skull and larynx in a felid species with a fully ossified hyoid (schematic drawing by Anne Dahm). E = epiglottis; La = larynx; Tr = trachea; labeling of hyoid bones as in Fig. 1

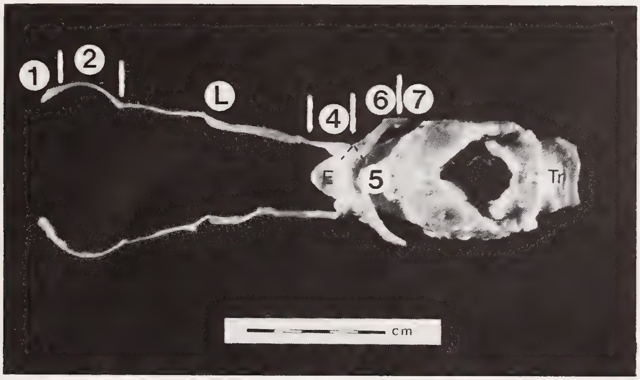

Fig. 3. Hyoid apparatus (still attached to the larynx) of a leopard (*Panthera pardus*) ad. ♀ (ZFMK 89.478), a species in which the hyoid is not fully ossified. The epihyoid is replaced by an elastic ligament (L). Other labeled structures as in Figs. 1 and 2; the tympanohyoid is cartilaginous; scale 5 cm. (Border between body of hyoid and its caudal and cranial cornu is marked on the bones for better visibility)

et al. 1977). The four hyoid specimens in Figs. 1 and 3 clearly show that in these felids the tympanohyal is not bony. In the present paper the statement of a fully ossified hyoid pertains to the hyoid elements 2 to 6 as shown in figures 1 and 2.

To extend and consolidate the hypothesis of a correlation between hyoid structure and vocalization in the Felidae, Pocock (1916: 229) stated: "Apart from the roar there is another very distinctive feature about the voice of the cats with a normal (i.e. fully ossified [G. P. and M. H. H.]) hyoid. This is the familiar 'purr'. Lions, tigers, leopards and jaguars never purr; on the other hand, such widely different species as cheetahs, pumas, caracals, jaguarondis, and others ... express ... that sound. These are interesting differences correlated with the differences in the hyoidean apparatus described above ... The species in which the hyoid is provided with this ligament (instead of the bony epihyale [G. P. and M. H. H.]) roar, but do not purr. All the other species of Felidae with normally constructed hyoid purr, but never roar."

In his later study on the classification of the existing Felidae, Pocock (1917b) considered these differences so important that they are the major criteria which separate two subfamilies of the Felidae, the Felinae and Pantherinae. The cheetah, as the sole species of the third subfamily, Acinonychinae, is thought to be more closely related to the Felidae, because it resembles them in the structure of its hyoid (cf. Fig. 1c with 1a and b).

Many later studies presenting a classification of the Felidae or dealing in detail with felid systematics largely followed Pocock's (1917b) concept based on the division of "roaring" and "purring" cats (e.g. Neff 1982). Even very recent biochemical studies in this field (e.g. Wayne et al. 1989) include these criteria in their discussion. In a list of the classification of the recent Carnivora, Wozencraft (1989) retained the Felidae and Pantherinae as subfamilies of the Felidae but with a content quite different from Pocock (1917b), e. g., the Pantherinae also including the lynxes (genus *Lynx*) and the caracal, the marbled cat (*Felis marmorata*) and clouded leopard (*Neofelis nebulosa*). Wozencraft (1989) did not go into detail on the decisive criteria for his system of classification but in the main he followed Collier and O'Brien (1985), O'Brien et al. (1987) and Wayne et al. (1989) who based their classifications on karyological, albumin immunological distance and isozyme genetic distance data. Yet the reference cited (Werdelin 1983) for the inclusion of the marbled cat in the Pantherinae does not present any data to support this hypothesis.

In his major study of felid skull morphology, Haltenorth (1937: 235) expressly questioned the significance of hyoid structure in felid systematics and considered roaring as a plesiomorphic vocalization character in species of this carnivore family. In a very recent study of felid skull morphology Salles (1992) included hyoid structure as a character and considered a fully ossified hyoid as the plesiomorphic state, but did not recognize subfamilies within the Felidae.

The current study tries to bring together all available data to test Owen's (1834) and Pocock's (1916, 1917b) original hypothesis that there is a correlation between hyoid structure and the presence of certain vocalizations in species of Felidae. Furthermore, this study discusses the findings of Hast (1986, 1989) on laryngeal anatomy with respect to vocalization and hyoid structure in felid species. In doing so, it will also provide a basis for evaluating the validity of using these character sets as criteria in felid systematics.

Material and methods

This study, being largely a review, is based on data published in the main papers cited on hyoid structure (Owen 1834; Pocock 1916), laryngeal anatomy (Hast 1986, 1989) and vocalization (Peters 1978, 1980, 1981, 1983, 1984, 1987) in the Felidae. In addition, supplemental data on hyoid structure, laryngeal anatomy and vocalization are also included. Table 1 lists the felid species for which respective data are available.

Data on hyoid structure and vocalization are present for all species listed; laryngeal anatomy is

known in a smaller number. Although the sample size for hyoid structure and laryngeal anatomy in some species is limited to only one specimen, it seems fairly safe to assume that the sample is representative of each species and, more certainly, the family Felidae altogether with respect to these character complexes. The amount of data on vocalization in the individual species is different. There is no species for which a comprehensive structural and functional analysis of its complete acoustic signal system exists. Therefore, statements on vocalization are made with reservations, especially for those species for which only limited data are available (see Tab. 1). Nevertheless, the data on vocalization for the family Felidae, as a whole, are considered sufficient for a comparative survey.

Table 1. **Data base on hyoid structure, laryngeal anatomy, and vocalization in the Felidae**

Species	Hyoid structure	Laryngeal anatomy	Vocalization
Acinonyx jubatus	+	+	+
Felis aurata	+	–	+
F. bengalensis	+	–	+
F. chaus	+	–	(+)
F. colocolo	+	+	(+)
F. concolor	+	+	+
F. geoffroyi	+	+	(+)
F. manul	+	+	(+)
F. margarita	–	–	(+)
F. marmorata	+	+	(+)
F. nigripes	+	+	+
F. pardalis	+	–	(+)
F. planiceps	+	+	(+)
F. rubiginosa	–	–	(+)
F. serval	+	+	+
F. silvestris	+	+	+
F. temmincki	–	–	(+)
F. tigrina	+	+	(+)
F. viverrina	+	–	(+)
F. wiedii	+	–	(+)
F. yagouaroundi	+	+	+
Lynx caracal	+	–	+
L. lynx	+	–	+
L. rufus	+	+	+
Neofelis nebulosa	+	+	+
Panthera leo	+	+	+
P. onca	+	+	+
P. pardus	+	+	+
P. tigris	+	+	+
P. uncia	+	+	+

+: character complex studied; –: not studied; (+): limited data [a qualification only used in the 'Vocalization' column in species with poorly known vocal repertoire].

Results and discussion

Hyoid structure and vocalization

Since the early investigations of Owen and Pocock did not deal with vocalization in a technical manner, there have been few serious attempts to define "roaring" as a vocalization of lions and other felid species, in appropriate technical terms. Therefore, it can be assumed that the term "roaring" has usually been applied in its "common use" dictionary definition, e.g. Merriam-Webster (1986: 1963): "roar: to utter or emit a full loud heavy prolonged sound ⟨ the lions roared ⟩" resp. "roar: the sound of roaring: the deep loud cry of some wild beasts ⟨ the roar of a lion ⟩", or Oxford English Dictionary (1933): "roar: 1. a full, deep, prolonged cry uttered by a lion or other large beast, . . ." Thus, in the

context of a technical description of felid vocalization, this is a circular definition and is equivocal, in that lions can produce different types of sounds which fit this general description. All the more, therefore, using the term "roaring" for vocalizations of other felid species is equivocal. Definitions in some recent publications like "The roar is a distinct, specific vocalization, very loud and resonant, which is produced by the pantherines – the lion, tiger, jaguar, and leopard." (Neff 1982: 20), obviously have the same weakness as those given above, and give no criteria for an unequivocal identification of the "roar" in any of these species.

Whereas Owen did not got into detail on roaring, and thus a critical evaluation of his statement in this respect is not possible, Pocock's (1916) denotation of roaring in different *Panthera* species but the snow leopard is specific enough to identify those vocalizations for which he used this term (i.e. vocalizations unique to the lion, jaguar, leopard, and tiger). Based on structural analyses (Peters 1978), it has been shown that certain of the relevant single calls of all four species and of the call types composing the structured call sequences in the first three species, which Pocock lumped under 'roaring', actually represent different types of vocalizations. Some of these vocalizations are not common to all four of these species, while others are common to many more species of the Felidae. Thus, Pocock's use of the term "roar" was ambiguous and his hypothesis of a correlation between hyoid structure and the presence of roaring in a species' acoustic repertoire needs to be reformulated and re-examined.

Leyhausen (1950) was the first who attempted to deal with felid roaring in a more technical way, but he did not go into much detail on vocalization structure. However, he pointed out differences in the sound of roaring and its articulation between lion and tiger, and the significance of roaring of hybrids between these two species for the elucidation of differences between the equivalent calls of their parental species. Reschke (1960, 1966), Tembrock (1962), Schaller (1972), and Hemmer (1966, 1968) published definitions of roaring in the Felidae, with the former three authors basing their definitions on bioacoustical analyses.

Referring to Schenkel (1966), Schaller (1972: 105), in describing roaring in lions, stated that "Roaring represents a graded system, ranging from barely perceptible grunts to full roars, . . ." This definition of roaring includes different types of single calls, either produced in a loud structured call sequence, as roaring "proper", or singly or in series of variable composition and temporal structure at low to medium intensity. Schenkel's (1966: 617, 618) original text, in discussing different types of roaring, did not differentiate between roaring as a structured call sequence and the single calls composing the sequence and their specific character. However, he clearly stated that he did not regard all call types involved as belonging to the same graded system. In an earlier treatment of vocalization in the tiger, Schaller (1967: 258) held that "Moans and roars are lumped into one category because the sounds represent variations in intensity of the same basic vocalization." Therefore, as in the lion, the term "roaring" in the tiger is applied to different types of single calls as well as to call sequences composed of such calls. Using "roar" in this way, Schaller very likely held that these vocalizations are fully equivalent in both species; he also listed (Schaller 1972: 452) the leopard as being able to roar. In effect, the ambiguous use of the term roaring was continued by Schenkel (1966) and Schaller (1967, 1972).

Reschke (1960, 1966) and Tembrock (1962) both used the German term for roaring ("Brüllen"), with qualifications, and pointed out its ambiguity. In defining different call types and the structured call sequences of certain felid species, they presented unequivocal characterizations of most relevant vocalizations in the *Panthera* species and some other felids but did not comment at all on the postulated correlation of the presence of roaring in a species and its hyoid structure.

Though not based on proper bioacoustic analyses, Hemmer (1966) presented a relatively clear definition of roaring in the lion, leopard, jaguar, and tiger. Because he was well

aware of the composite nature of the structured call sequences in the lion, leopard, and jaguar and the absence of an equivalent call sequence in the tiger, he aimed at a definition of roaring that would encompass all four species. Thus, the typical roaring sequence of a lion, as commonly understood (very likely also by OWEN and POCOCK in their relevant publications), was not defined as roaring in its entirety but only its intense initial portion (HEMMER 1966: 60–61). Under this object-defined definition of roaring, HEMMER (1966) held that the lion, leopard, jaguar, and tiger do roar, whereas the snow leopard does not roar. In making such a statement this author neglected the differences between the former four species in respect of temporal and intensity patterning of the relevant call series. HEMMER (1966: 76) concluded that, in felids, there is no direct correlation between hyoid structure and vocalization. He based this conclusion on his observation that the snow leopard is able to purr and unable to roar, despite the fact that its hyoid is not fully ossified; this would predict just the opposite situation for these two vocalizations.

In a detailed technical study of vocalization in all *Panthera* species, the clouded leopard and puma *(Felis concolor)*, PETERS (1978) did not apply the equivocal term 'roar' as it had been used for different types of vocalizations in various species. For the lion, in which 'roaring' usually was applied to the loud species-specific structured call sequence (see Figs. 4, 5), PETERS (1978) demonstrated that these sequences comprise at least two different types of calls (Figs. 6, 7), one of which is definitely not found in the tiger. All three (very rarely four) call types, however, which can appear in a roaring sequence of the lion may

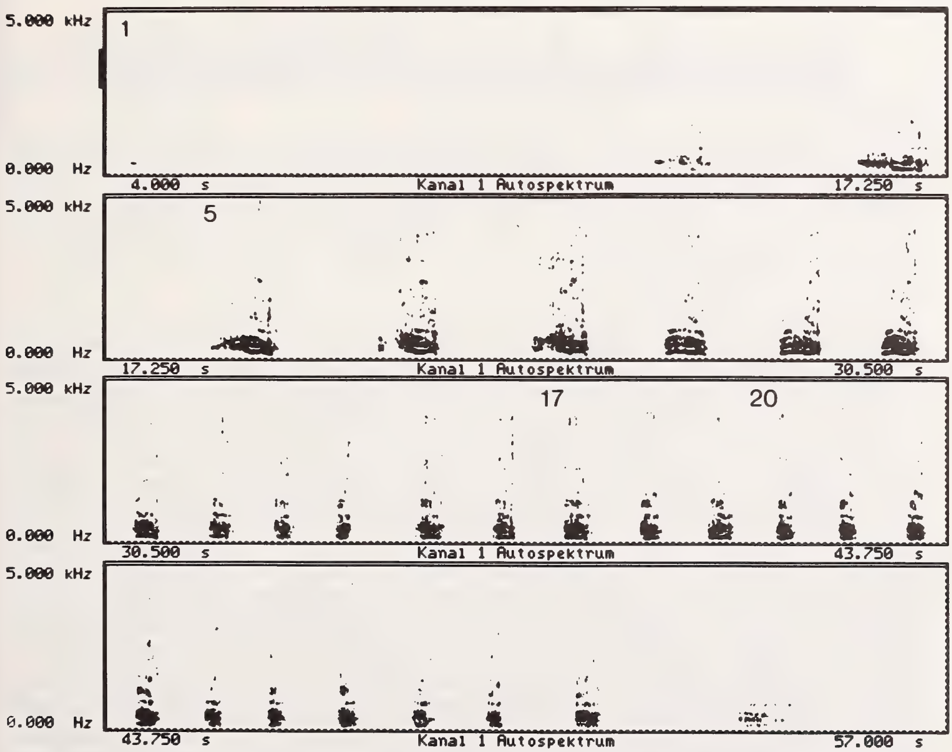

Fig. 4. Continuous sonagram (53 s, partitioned over 4 sonagrams of equal duration) of a complete roaring sequence ('roaring proper') of an adult ♂ lion (*Panthera leo*). Frequency axis (y-axis) represents 5 kHz, time axis (x-axis) 13.25 s in each sonagram. Labeled single calls no. 5 (see Fig. 6) and 17–20 (see Fig. 7) are analyzed once again in more detail

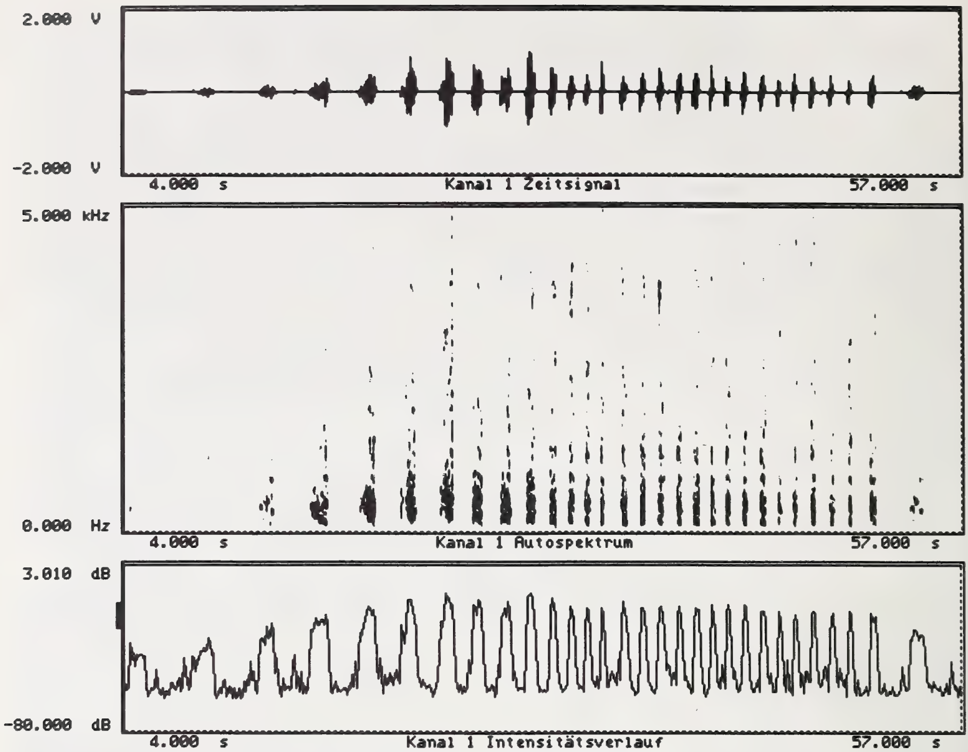

Fig. 5. Oscillogram (top), sonagram (middle) and intensity graph (bottom) of the same roaring sequence as in Fig. 4. X-axis (time) is the same for all (53 s duration), units and their respective calibrations on the y-axes are given. The call types composing the sequence, their succession, the general pattern of their change in intensity, duration and duration of the intervals between them are species-specific for lion roaring

also be present in the equivalent sequence in the structured call series of the leopard and jaguar. The usual form of these series in the latter two species, though, is different from the roaring of lions in that they are equivalent to the second half of the lion roaring sequence.

Like Hemmer (1966), Peters (1978) concluded that hyoid structure and the occurrence of roaring in the Felidae (defined by reference to the lion's structured call sequence) are not correlated. Thus, with the relevant vocalization of the lion – as very likely understood by Owen and Pocock – as the standard of comparison, the leopard and jaguar have fully equivalent vocalization sequences, whereas the tiger and snow leopard do not. These are the only felid species with an incompletely ossified hyoid. Because of the established differences in the relevant call types and call sequences (under the various definitions of roaring), and as none of these is shared by all five species, and at the same time is not present in any other felid, an incompletely ossified hyoid in a felid species is not necessarily associated with the presence of roaring in this species' acoustic repertoire. Hence the hypothesized direct correlation of roaring and hyoid structure (i.e. an incompletely ossified hyoid) can be refuted. For the first time, this statement was based on technical analyses and definitions of all relevant sound types and call sequences (Peters 1978).

Similar ambiguity and confusion exist for the definition of purring, the 'counterpart' of roaring within the felid acoustic repertoire, as postulated by Pocock (1916). The Merriam-Webster (1986) dictionary definition of purr as "a low vibratory murmur of a

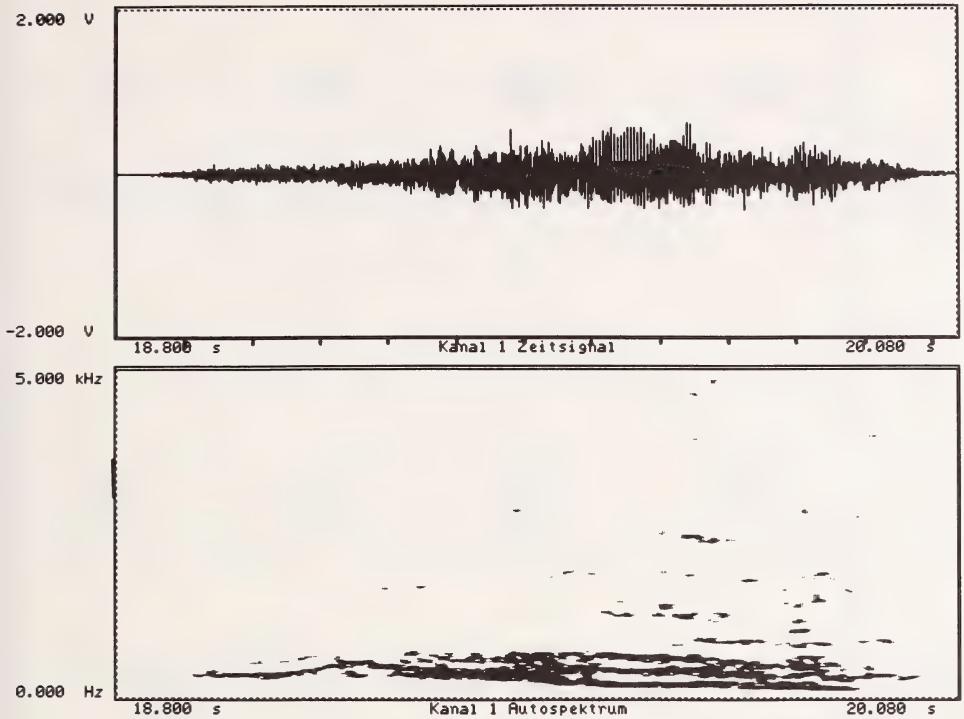

Fig. 6. Oscillogram (top) and sonagram (bottom) of call no. 5 of the roaring sequence shown in Figs. 4 and 5. X-axis (time) is the same for both graphs (1.28 s duration), its subdivisions in the oscillogram representing 0.1 s each. Units and their respective calibrations on the y-axes are given. This call is a main call with grunt element (cf. PETERS 1978)

cat that appears to indicate contentment or pleasure and is believed to result from the streaming of air over the false vocal cords" gives no criteria for an unequivacal structural identification of this felid vocalization, although even making a statement on the supposed mechanism of sound production. In principle, there ought to be less difficulty in correctly identifying purring, because it is such a familiar sound in the domestic cat. Moreover, some of its unique structural charasteristics are already identifiable by careful observation without proper bioacoustic analysis. The articulation and structure of purring are so singular that only a vocalization with all its pertinent characteristics (see FRAZER SISSOM et al. 1991), established by bioacoustic analysis (cf. Fig. 8), ought to be so classified.

Anecdotally, this vocalization has been reported in many felid species, even for most of those that allegedly cannot purr, like lion or tiger, and other *Panthera* species (e.g. HEMMER 1966, 1968; SCHALLER 1972; NEFF 1982). Several authors (e.g. HEMMER 1966, 1968; SCHALLER 1972) maintained that in some of these species purring is articulated during exhalation only. LEYHAUSEN (pers. comm.) holds that very young cubs of the *Panthera* species very likely are able to purr during in- and exhalation. It is highly probable that different types of sounds were lumped under the term 'purring' in various species. Verifiable evidence based on proper bioacoustical analyses for the existence of this vocalization was only presented for relatively few felid species: juveniles of margay *(Felis wiedii),* little spotted cat *(F. tigrina)* and bobcat *(Lynx rufus),* juveniles and adults of the domestic cat, jaguarundi *(Felis yagouaroundi),* puma and serval *(F. serval),* and adults of the Eurasian lynx *(Lynx lynx),* cheetah, and the Indian desert cat *(Felis silvestris ornata)*

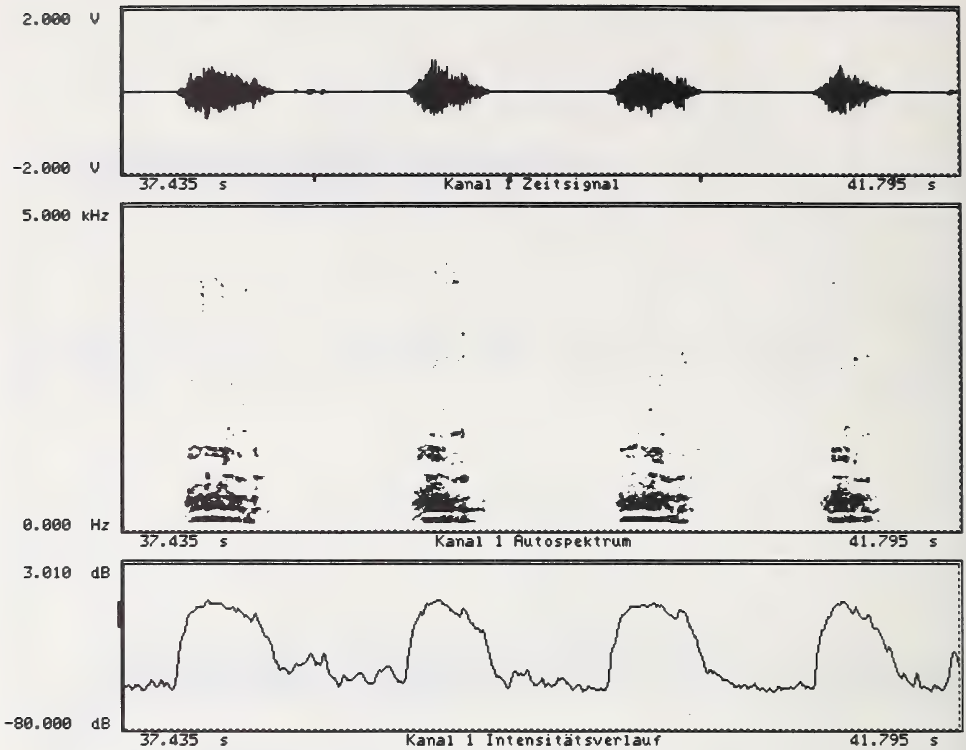

Fig. 7. Oscillogram (top) and sonagram (bottom) of calls no. 17 to 20 of the roaring sequence shown in Figs. 4 and 5. X-axis (time) is the same for both graphs (4.36 s duration), its subdivisions in the oscillogram respresenting 1 s each. Units and their respective calibrations on the y-axes are given. These calls are grunts (cf. PETERS 1978)

(PETERS 1981). All of these species have a fully ossified hyoid; unequivocal observations and tape recordings of purring in one further species of the Felidae with this type of hyoid morphology exist (see Tab. 2). However, a general statement on a direct correlation between the presence of a fully ossified hyoid in a felid species and its ability to purr can only be made with reservations, since unequivocal evidence of this sound is lacking in too many species of the Felidae which have this hyoid morphology. On the basis of available data, the existence of such a correlation also cannot be refuted, though. In deatiled analyses of domestic cat purring (REMMERS and GAUTIER 1972; FRAZER SISSOM et al. 1991), no mention was made of a role of the hyoid in articulating this sound. None of the five felid species with an incompletely ossified hyoid has been examined carefully enough to make a scientifically substantiated statement as to whether they can or cannot purr.

So far, no other vocalizations have been technically described in the Felidae, the distribution of which among the various species of the familiy matches that of the two hyoid structure types.

As detailed before, the postulated direct correlation of an incompletely ossified hyoid in a felid species and its ability to roar has been refuted. In respect of purring, a definitive statement cannot be made yet as to whether all species with a completely ossified hyoid can purr and whether this vocalization is restricted to these felids. Therefore, the hypothetical correlation of purring and hyoid structure in the Felidae can neither be falsified nor verified at the present state of analysis. Consequently, as this hypothesis is an attempt at explaining

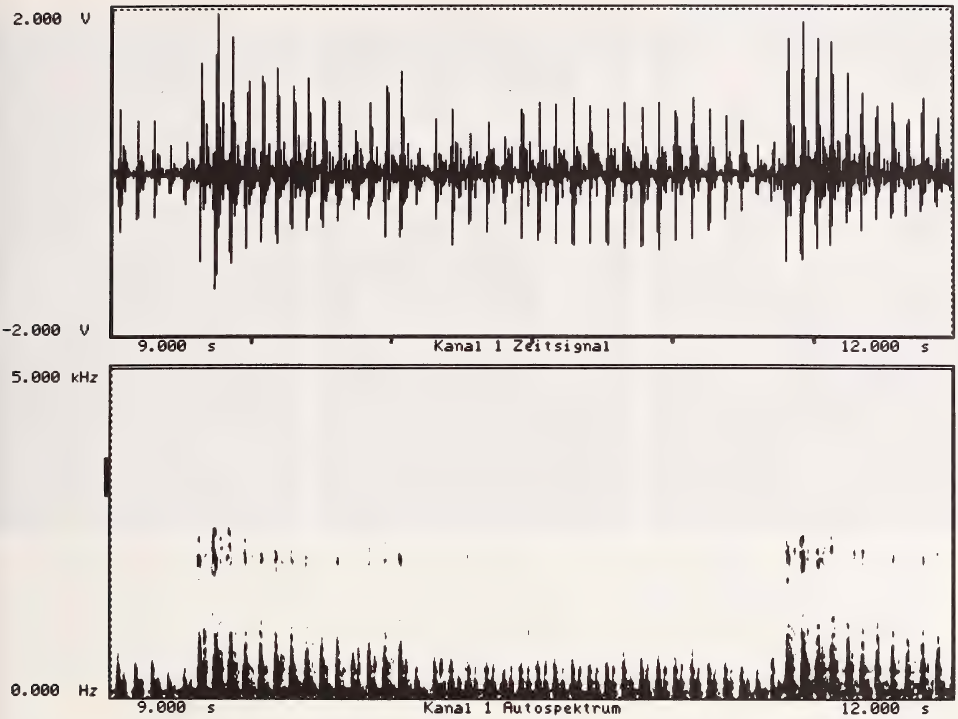

Fig. 8. Oscillogram (top) and sonagram (bottom) of purring of an adult ♀ puma (*Felis concolor*). X-axis (time) is the same for both graphs (3 s duration), its subdivisions in the oscillogram representing 0.5 s each. Units and their respective calibrations on the y-axes are given

the cause of major differences in the composition of acoustic signal systems in felids, it seems to be scientifically more appropriate, for the present, not to maintain it.

Laryngeal anatomy and vocalization

Detailed comparative anatomical studies of the larynx as the sound producing organ had been lacking in the Felidae until very recently (Hast 1986, 1989). Earlier studies of felid larynges by Negus (1949), Kelemen (1963) or Schneider (1964) did not deal with the interdependence of larynx structure and the acoustic repertoire of a species in a specific way. They only arrived at statements like "The roar of the lion is produced with a comparatively simple vocal apparatus." (Kelemen 1963: 503) or "The larynx of the felids in general is more primitively constructed than the larynx of the hare or of the antelope, but in spite of this the vocal production of the latter is very much poorer." (Kelemen 1963: 514). This lack of information exists despite the fact that the hypothetical correlation of hyoid structure and vocalization in the Felidae already was a relatively common view.

The major findings of Hast (1989: 118, 119) are that, of the 14 felid species studied, the larynges of lion, leopard, jaguar, and tiger are exceptional in having a "large pad of fibro-elastic tissue which constitutes the rostral portion of each of the proportionately very large undivided vocal folds". The other species studied are not atypical for carnivores in that they have a "larynx with divided thyroarytenoid folds, with a depression between the rostral and the caudal folds that varies from a slight fossa to a deep ventricle, and a vocal fold with a sharp edge" (see Fig. 9 a–c). The specific structure of thick vocal folds in the

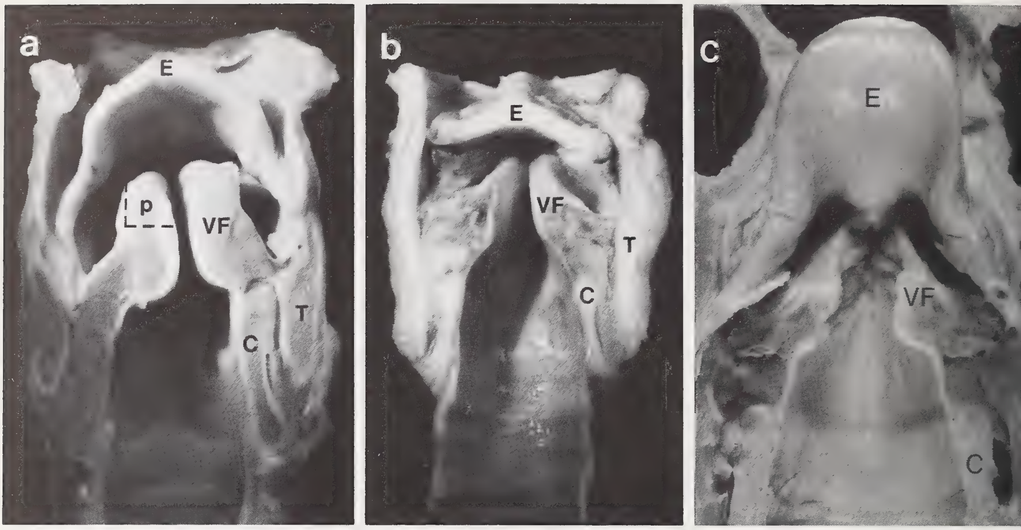

Fig. 9. Dorsal view of larynges of a: a jaguar (*Panthera onca*), b: a snow leopard (*P. uncia*), and c: a puma (*Felis concolor*) cut coronally. The longitudinally very large vocal folds (VF) of the jaguar with their large pad of fibro-elastic tissue (p) are readily distinguished from the proportionately shorter vocal folds of the snow leopard and the even shorter vocal folds of the puma with their sharp edge (E = epiglottis; C = cricoid cartilage; T = thyroid cartilage). (Figures a and b from Hast [1989] with kind permission of the Journal of Anatomy; c: reproduced at a larger scale than a and b)

four species mentioned has the consequence that they are able to produce sounds of high acoustical energy and with lower frequency components than those species with thinner vocal folds (Hast 1989). Additional felid species (*Felis colocolo, F. nigripes, F. serval, F. tigrina, F. yagouaroundi*) studied subsequent to Hast (1986, 1989) confirm that only the four species mentioned above have this special morphology of the vocal folds.

The incompletely ossified hyoid also enables lion, leopard, jaguar, tiger, and snow leopard to move their larynx away from the oral cavity, and thus also from the mouth, thereby extending the length of the tube (see Fig. 10 B), which results in an even lowered pitch of vocalization. Consequently, the specific structure of their hyoid can amplify the effect of the thick vocal folds in the former four species quantitatively. However, it is not possible at present to quantify the effect of their unusually shaped vocal folds in deepening and intensifying the calls of these four species.

Generally, species of the Felidae vary considerably in the pitch of their equivalent calls, and no uniform, direct size-correlation is manifest in an interspecific comparison. On the contrary, some felid species with sharp-edged vocal folds (and a completely ossified hyoid) have strikingly high- and low-pitched calls in relation to their position within the over-all size range of the Felidae (this statement also holds for the snow leopard with an incompletely ossified hyoid). In relation to its size, this species' main call is remarkably high-pitched (Peters 1978). This finding is a caveat that vocal fold morphology (and hyoid structure) alone are not decisive parameters for the pitch of a felid species' calls.

With the exception of a few measurements for lions (Jarofke 1982), no quantitative data on loudness of felid vocalizations are available; therefore no interspecific comparisons in this respect can be made. Generally, none of the morphological and physiological parameters determining the pitch and intensity of a felid species' vocalizations have been quantified.

Hast (1986, 1989) observed that the specific structure of the vocal folds in the lion,

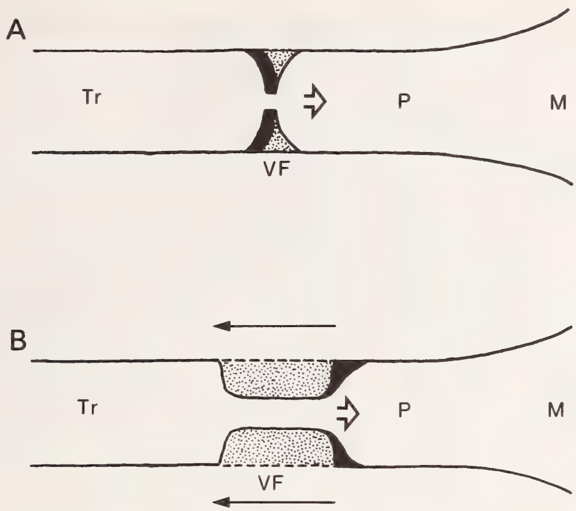

Fig. 10. Schematic drawing of the vocal tract of A: a felid species with sharp-edged vocal folds and B: a felid species with vocal folds with a large pad of fibro-elastic tissue. The open arrows in A and B show the direction of the expiratory air flow. The arrows in B indicate that a hyoid with an elastic ligament instead of a bony epihyoid, which the species with this type of vocal fold morphology have, allows for an elongation of the supraglottal vocal tract, i.e. the distance of the sound generator from the mouth, which results in lower pitch of calls (M = mouth; P = pharynx; Tr = trachea; VF = vocal folds)

tiger, leopard, and jaguar has a qualitative influence on their vocal repertoires, enabling them to roar (although not technically defined). Therefore, according to the above discussions it is not clear to which vocalization(s) this term actually refers in these four species. As detailed before, no matter how roaring was defined by any of the earlier authors, it is not exclusively common to these four species among the Felidae. If the hypothesis of a correlation between vocal fold morphology and vocalization in the Felidae is maintained, to the effect that these morphological characteristics have a qualitative influence on the composition of the vocal repertoire of species, the distribution of vocalization types must be examined. This distribution must be compared to that of the different types of vocal folds in the various species of this carnivore family, especially lion, leopard, jaguar, and tiger, in contrast to the rest of the family. There is but one type of vocalization, the main call with grunt element (Fig. 6), which is common to these four species but not present in any other felid species (Peters 1978). This call type is a constitutive element in the structured call sequences of the lion (= roaring 'proper') (Figs. 4, 5) and may be present in the equivalently structured call sequences of leopards and jaguars. Tigers utter such calls as single calls or in call series which are irregular with respect to the call types that compose them, the calls' intensity and their temporal sequence (Peters 1978). Parallel with this character complex, the larynges of these four species have morphological characteristics in common, which distinguish them from those of all other felid species, specifically a large pad of fibro-elastic tissue which constitutes the rostral portion of proportionately very large vocal folds (Hast 1989). However, this concordance/association of characters is not unequivocal evidence that the occurrence of this specific type of vocalization in only these felid species is caused by their special laryngeal morphology. At the present state of analysis no other type of vocalization is known which is shared only by the four species with specific vocal fold type, as opposed to the equivalent character situation in the rest of the species of the family Felidae. Therefore, a qualitative

Table 2. **Association of characters of hyoid structure, anatomy of vocal folds and vocalization in species of the Felidae**

Species	Hyoid structure	Vocal fold type	Roar	Vocalizations Purr	MC
Acinonyx jubatus	os	s	–	+	–
Felis concolor	os	s	–	+	–
F. geoffroyi	os	s	–	+	–
F. serval	os	s	–	+	–
F. silvestris	os	s	–	+	–
F. tigrina	os	s	–	+	–
F. wiedii	os	?	–	+	–
F. yagouaroundi	os	s	–	+	–
Lynx lynx	os	?	–	+	–
L. rufus	os	s	–	+	–
Neofelis nebulosa	os	s	–	?	?
Panthera uncia	e	s	–	–	–
P. tigris	e	p	–	–	+
P. leo	e	p	+	–	+
P. onca	e	p	+	–	+
P. pardus	e	p	+	–	+

MC: main call with grunt element; os: hyoid completely ossified; e: hyoid with elastic ligament; s: sharp edged vocal folds; p: vocal folds with thick pad of fibro-elastic tissue; character +: present; –: absent; ?: no data/character state doubtful.

influence of vocal fold morphology on a species' vocalization repertoire remains conjectural in the Felidae.

Hyoid structure, laryngeal morphology, and vocalization as characters in felid systematics

Since initial studies by Pocock (1917b), hyoid structure (and its correlation with vocalization) has remained a major criterion in felid classification above the species level (e.g. Corbet 1978; Neff 1982). After discussing statements by various authors that lions, tigers, leopards, jaguars and snow leopards (the felid species with an incompletely ossified hyoid which allegedly ought to be unable to purr) can purr, Neff (1982: 21) concluded "... there is still some doubt about the distribution of the ability to purr among the wild cats." Although she cited data that would refute the postulated correlation of hyoid structure and the presence of roaring or purring in a felid species, Neff (1982) retained Pocock's criterion of hyoid structure to separate the subfamilies. Thus, she either regarded the differences in hyoid structure as sufficient to separate the subfamilies of the Felidae, irrespective of whether there is a correlation with vocalization or not – as verified above there is not –, or she doubted reports of purring in species which allegedly are not able to produce this sound because of their hyoid structure. Even very recent classifications of the Felidae based on character complexes like immunological distance or DNA-hybridization data (Wayne et al. 1989) refer to the differences in hyoid structure as supporting evidence. Haltenorth (1937), however, expressly denied any systematic significance of hyoid morphology within the Felidae.

If the incomplete ossification of the hyoid is considered as a derived character within the Felidae (cf. Salles 1992), the monophyletic group characterized by this synapomorphy would include lion, leopard, jaguar, tiger, and snow leopard, irrespective of the rank attributed to this taxon and other characters allegedly/perhaps correlated with hyoid structure. According to various authors, additional synapomorphic characters shared by these five species are: 1. coat pattern on the head completely dissolved into spots (Hemmer

1981) (other authors like Leyhausen [1950] hold another view in respect of this character); 2. bridge of the nose covered with hair up to its anterior edge (Hemmer 1981); 3. simple structure of the baculum without bifurcation in its basal portion (Kratochvíl 1976).

In addition to the above mentioned five species Hemmer (1978) included marbled cat and clouded leopard in the 'pantherine line', based on morphological (see Pocock 1917a, 1932), ethological, physiological, and karyological data. However, in a later publication on the same topic (Hemmer 1981), the 'pantherine line' did not include the marbled cat. Based on coat colour and pattern, Weigel (1961) grouped *Panthera, Uncia,* and *Neofelis* in the Pantherinae. In addition to the five species united in this subfamily by Pocock (1917b), Stains (1984) included the clouded leopard without giving criteria for doing so; Wozencraft (1989) included lion, leopard, jaguar, tiger, snow leopard, clouded leopard, the marbled cat, the lynxes and the caracal in the subfamily Pantherinae. Based on their comparative biochemical studies Collier and O'Brien (1985), O'Brien et al. (1987) and Wayne et al. (1989) established a '*Panthera* lineage' with the five roaring (sic) cat species (lion, leopard, jaguar, tiger, snow leopard), the lynxes, and the marbled cat, all of which also share an identical karyotype different from the remaining felid genera (cf. Wurster-Hill and Centerwall 1982). In addition, the '*Panthera* lineage' of Collier and O'Brien (1985) includes – among others – such diverse species as the African golden cat *(F. aurata),* serval, cheetah, and yagouaroundi *(F. yagouaroundi).*

However, illustrating again the conceptual confusion with regard to 'roaring', Wayne et al. (1989: 473) listed further characters supporting their classification of the Felidae in stating that "The most recent radiation led to the five species of roaring cats, genus *Panthera*, . . .", and then continue (473, 474) "The lion, tiger, leopard, and jaguar have an incompletely ossified hyoid that allows them to roar and thus unites the group. . . . the snow leopard *(P. uncia),* the only nonroaring member of the genus, . . . has a hyoid with structural similarities to the pantherids." (sic).

Hast (1986, 1989) considered the systematic significance of the distribution of the two basic types of vocal fold morphology within the Felidae, especially as regards the content of the genus *Panthera* and the generic association of the snow leopard. Shared acoustical and morphological characteristics in lion, leopard, jaguar, and tiger (presence of main call with grunt element, hyoid structure, vocal fold morphology), may support their joint classification in the genus *Panthera.* The snow leopard shares only one of these three characteristics with the latter four species, the incompletely ossified hyoid. These findings may be taken to support the view of various authors (e.g. Pocock 1917b; Haltenorth 1937; Hemmer 1966, 1968, 1972, 1981; Peters 1978, 1980; Neff 1982) that the snow leopard should be classified in its own genus *Uncia* and not in *Panthera* (Honacki et al. 1982; Corbet and Hill 1991).

The continuing dispute on the systematics of the Felidae (cf. e.g. Simpson 1945; Ewer 1973; Hemmer 1978; Leyhausen 1979, 1992; Král and Zima 1980; Honacki et al. 1982; Kratochvíl 1982; Collier and O'Brien 1985; Wayne et al. 1989; Wozencraft 1989; Corbet and Hill 1991; Kitchener 1991; Nowak 1991; Salles 1992) is clear evidence that conclusions drawn concerning this matter vary according to character complex(es) studied and their weighting, in view of differences and conformities of character/character state distributions found in species for various complexes.

Together with other morphological character complexes studied, data on hyoid structure, vocal fold morphology and especially vocalization support the hypothesis that *Panthera, Uncia* and *Neofelis* form a monophyletic group (cf. Hemmer 1981; Salles 1992). These characters conflict with chromosomal (Král and Zima 1980) and immunological distance data (Collier and O'Brien 1985), which would ally the lynxes and the marbled cat to this group.

Systematic studies based on any set of genetically determined characters should be congruent with other such studies based on different sets of characters in the same

organisms (Hillis 1987). The conflict in the Felidae is very likely due to unrecognized character convergencies, mistakes in the interpretation of shared characters/character states as symplesiomorphic or synapomorphic, and the fact that the different character complexes undergo different rates of evolution, with character evolution not generally reflecting group phylogeny. We have not yet arrived at a stage of analysis of the evolutionary history of the Felidae in which congruence/consensus or complementarity of the various character data sets are possible.

Acknowledgements

Both authors would like to express their sincere thanks to the staff members of the zoos and museums who kindly provided postmortem specimens of cut larynges: Cheyenne Mountain Zoo, Field Museum of Natural History, Florida State Museum, Jersey Wildlife Preservation Trust, Lincoln Park Zoo, Little Rock Zoo, Milwaukee Zoo, National Zoological Park, Wildlife Safari of Oregon, Wuppertal Zoo, Zoological Society of San Diego. We also very much appreciate the time given by Dr. Rainer Hutterer, Professor Dr. Paul Leyhausen, and Dr. Bruce D. Patterson to critically review this paper prior to its submission for publication. G. P. thanks the preparators at his institute for their careful and skilled work in preparing larynx and hyoid specimens, Mr. H. Meurer for doing the photographs and Miss A. Dahm for the drawings.

Zusammenfassung

Hyoidbau, Kehlkopfmorphologie und Lautgebung bei Feliden (Mammalia: Carnivora: Felidae)

Bei den meisten Arten der Feliden ist das Hyoid (Zungenbein) vollständig verknöchert, bei fünf Arten der Familie jedoch nicht, sondern enthält ein elastisches Ligament. Dieser Unterschied im Hyoidbau wurde von vielen Autoren als Ursache für die Ausbildung bzw. das Fehlen der beiden Lautformen Brüllen und Schnurren im Lautrepertoire der einzelnen Arten der Felidae angesehen. Hyoidbau und damit hypothetisch korrelierte Lautgebung wurden in der Systematik der Felidae als wesentlicher Merkmalskomplex bewertet. Die vorliegende Untersuchung diskutiert die postulierten Zusammenhänge zwischen Hyoidbau und Lautgebung auf der Grundlage eindeutig definierter Lauttypen und bezieht dabei neue Ergebnisse zur Kehlkopfmorphologie der Feliden mit ein.

Es ist erwiesen, daß nicht alle fünf Felidenarten mit einem unvollständig verknöcherten Zungenbein brüllen können, ein solcher Hyoidbau bedingt also nicht automatisch die Ausbildung des Brüllens. Andererseits findet sich diese Lautform aber auch bei keiner Art mit einem vollständig verknöcherten Hyoid. Alle Arten, bei denen bisher die Fähigkeit zu schnurren gesichert ist, haben ein vollständig verknöchertes Hyoid, für viele Arten mit diesem Hyoidtyp fehlt allerdings bisher noch der eindeutige Nachweis dieser Lautform, so daß eine definitive Aussage darüber, ob ein solcher Hyoidbau für die Ausbildung des Schnurrens notwendig ist und diese bedingt, bisher nicht möglich ist. Das Vorkommen eines weiteren Lauttyps ist auf die vier Felidenarten beschränkt, deren Stimmlippen eine von allen übrigen Arten der Familie abweichende Form aufweisen. Die Aussagefähigkeit dieser Merkmalskomplexe für eine Rekonstruktion der stammesgeschichtlichen Beziehungen innerhalb der rezenten katzenartigen Raubtiere wird erörtert.

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Authors' addresses: Dr. GUSTAV PETERS, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany; Prof. Dr. MALCOLM H. HAST, Northwestern University Medical School, 303 East Chicago Avenue, Chicago, Illinois 60611, USA

Z. Säugetierkunde 59 (1994) 105–115

ISSN 0044-3468

Oral suction of a Pacific walrus (*Odobenus rosmarus divergens*) in air and under water

By R. A. Kastelein, M. Muller, and A. Terlouw

Harderwijk Marine Mammal Park, Harderwijk, Holland

Receipt of Ms. 1. 4. 1993
Acceptance of Ms. 21. 6. 1993

Abstract

Walruses mainly eat sessile bentic prey. Of bivalve molluscs, usually only the siphons and feet are found in walrus stomachs, and it is thought that walruses use oral suction to separate the molluscs from their shells. Low pressure in the buccal cavity is caused by retraction and depression of the tongue which acts like a piston. The pressure in the oral cavity of a female walrus was measured during several in-air and underwater suction tests. The lowest pressure recorded in air was −87.9 kPa (−0.879 Bar, almost vacuum) when the walrus sucked on the pressure transducer. The lowest pressure recorded under water was −118.8 kPa (−1.188 Bar) when the walrus was sucking on a mackerel. The walrus has good control over its tongue muscles and over both the pressure and the duration of suction.

Introduction

In contrast to most pinnipeds which prey on fish and squid, walruses mainly eat sessile bentic prey (Fay 1982). Of bivalve molluscs, usually only the siphons and feet are found in walrus stomachs. The bodies may be digested so quickly that they are difficult to detect. Vibe (1950) suggested that walruses use suction to separate the molluscs from their shells. Evidence to support this hypothesis was given by Oliver et al. (1983, 1985) who found intact empty shells on both sides of furrows in the ocean floor in walrus foraging areas. Kastelein and Mosterd (1989) observed walruses feeding on bivalve molluscs in a sandy substrate in a pool and leaving the empty shells on the bottom. Fay (1982) suggested that low pressure in the buccal cavity could be caused by retraction and depression of the tongue which could act like a piston. Kastelein and Gerrits (1990) showed that the buccal cavity of the walrus is relatively large due to the curvature of the maxilla and hard palate, and Kastelein et al. (1991) described the well-developed tongue muscles which are involved in producing oral suction.

The retraction speed of feet and siphons of molluscs depends on the species but the process is also temperature dependent. There is good evidence that *Serripes* (*Cardium*) *groenlandicus* is comparitively slow in retracting its feet. This may allow the walrus to remove the feet, and possibly the attached body, before they have retracted into the shells (Mansfield 1958). The suction force of the walrus, required to separate the body or body parts from the shells, probably depends on the degree of retraction and closure of the clam. It is probable that beyond a certain state of retraction, the Walrus is unable to extract the edible parts.

After detecting an object on the ocean floor, a walrus has a limited amount of time to identify (Kastelein and van Gaalen 1988; Kastelein et al. 1990), in certain cases excavate (Oliver et al. 1983; Kastelein and Mosterd 1989) and position the prey item between its lips (Kastelein et al. 1991), if it is to use the suction technique succesfully with a clam. This foraging technique has to be efficient because adult walruses in oceanaria eat about 50 kg of food per day (Kastelein pers. obs.). This would be about 3000 adult sand gapers (*Mya arenaria*) with an average soft body weight of 17 g. Born and Knutsen

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(1990) even found 6401 individual prey items in a walrus stomach. A bivalve may detect the vibrations or current caused by an approaching walrus sooner than the walrus detects the clam, so the retraction of foot and siphon may have begun by the time the walrus touches the prey (Kristensen 1957). So, the amount of time available for food processing is governed by the detection distance and retraction speed of the mollusc, as well as by the identification and excavation speed and suction power of the walrus. The prey identification speed of walruses was studied in a psychophysical study by Kastelein and van Gaalen (1988). The present study investigates the parameters determining suction force.

Material and methods

Animal

The study was done with a 10-year-old female Pacific walrus (*Odobenus rosmarus divergens*, code OrZH004) which was born in the wild, arrived at Harderwijk in 1985 and which has participated in educational performances since then.

Study area

A 50 cm × 50 cm square hole was made in a door between the walrus quarters and an adjacent room. In this room, a 50 cm × 50 cm × 50 cm water trough was placed on the floor beneath the hole. The walrus was trained to put her head through the hole in the door and into the water in the trough on command.

Experimental procedure

To measure the pressure changes in the walrus' mouth a Millar PC 350 catheter pressure transducer was used. This pressure transducer was chosen, because it is small (1.67 mm diameter), it has a linear relationship between pressure and output voltage, a broad bandwidth (about 3 kHz) and it is stabilized for temperature effects (Van Leeuwen and Muller 1983). The output voltages were amplified with a differential amplifier (AD 610 K). The signals were stored on a Bell and Howell recorder (speed 30 inch/s, bandwidth 0–10 kHz), played back to be visualized on a Tektronix digital storage scope (type 2211) and plotted on a HP 7475A plotter (Hewlett-Packard).

The pressure transducer was inserted into a thawed fish. To protect the sensor, a hollow metal tube with a pointed end was first inserted through the body of the fish from the anus to the mouth. Then, the wirelike pressure transducer was threaded through the tube until the tip became visible. The tube was carefully removed and the sensor was placed so that its tip stuck out of the mouth of the fish by about 1 cm.

The pressure changes in the walrus' mouth were measured under various circumstances. When a fish containing the pressure transducer was held in front of the walrus' mouth, the animal gripped the rostral third part of the fish in its mouth, and then tried to suck it from the hand of the trainer (Fig. 1). The trainer kept a firm hold of two thirds of the fish until it broke or slipped from his hands. This could be done both in air and under water. Herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) 20 to 25 cm in length were used.

In air, the pressure transducer was also offered while held along the trainer's finger, the walrus having been trained to suck the finger. In air, the transducer could also be held perpendicular to the cheek of the trainer. The walrus had been trained to "kiss" the trainer, and thus to suck the transducer, which extended about 6 cm into the walrus' mouth cavity. Both sucking the trainer's finger and "kissing" his cheek were known behaviours to the walrus because they were used in educational performances. In other experiments, the pressure transducer alone was offered to the animal. In all experiments, about 6 cm of the catheter tip was inside the walrus' mouth during suction.

The suction curves produced in this study consist of a zero level which is equal to the ambient air pressure, a descending part in which the pressure is dropping due to the depression and retraction of the tonge, a section in which maximum pressure is exerted, and an ascending part in which the pressure is returning gradually to ambient pressure because air or an object slips, or water flows, into the mouth cavity. For an example see figure 2. The following parameters were calculated:

Amp 0 = ambient pressure.
Amp 90 = 90 % of the maximum amplitude.
Amp 10 = 10 % of the maximum amplitude (10 % below ambient pressure).
Amp dif = Amp 90 – Amp 10.
Amp max = maximum amplitude.
T10 = Duration of the suction event at Amp 10.

Fig. 1. The walrus sucking a fish containing the pressure transducer. The hole in the door is 50 × 50 cm (Photo: Henk Merjenburgh)

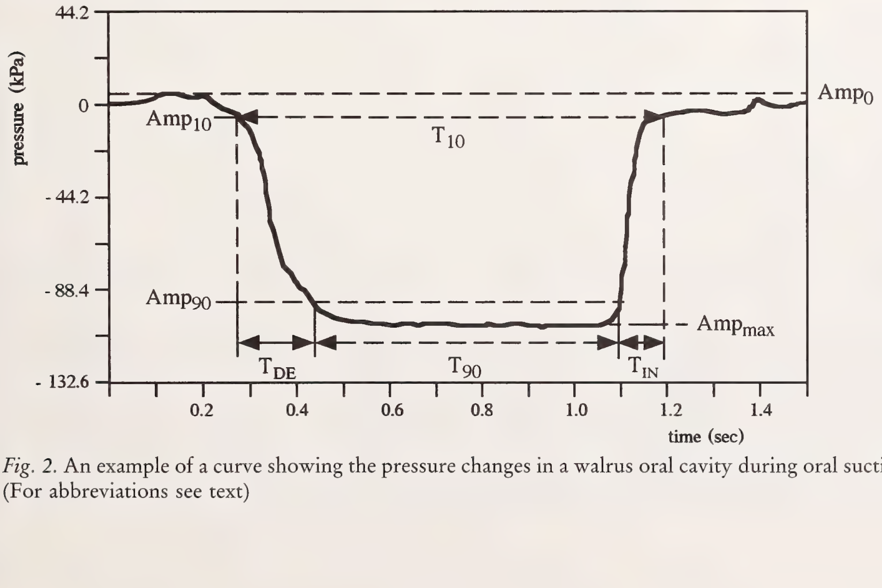

Fig. 2. An example of a curve showing the pressure changes in a walrus oral cavity during oral suction. (For abbreviations see text)

T90 = Duration of the suction event at Amp 90.
Tde = Time needed to decrease the pressure from Amp 10 to Amp 90.
Tin = Time needed to increase the pressure from Amp 90 to Amp 10.

Results

Table 1 shows the suction curve parameters for the different test situations which will be described in detail below.

Finger in air

On average the shortest T90 and smallest Amp 90 occurred when the walrus sucked the finger. A typical example of a suction curve is shown in figure 3A.

Cheek in air

On average the shortest T10, Tde and Tin and the largest Amp 90 occurred when the walrus "kissed" the trainer's cheek in air. Using this method, the suction parameters were less variable in each trial which is apparent from the relatively small standard deviations. A typical example of a suction curve is shown in figure 3B.

Table 1. **Average values (x) and standard deviations (S.D.) of suction parameters during a number of trials (N) in a 10-year-old female Pacific walrus**

Situation		In air				Under water
		Finger	Cheek	Transducer	Fish	Fish
Amp90	x	41	62	55	45	73
(kPa)	S.D.	18	11	19	6	24
	N	8	11	5	4	19
Amp10	x	5	7	6	5	8
(kPa)	S.D.	2	1	3	1	2
	N	8	11	5	4	19
Amp dif	x	36	55	49	40	65
(kPa)	S.D.	16	10	16	5	21
	N	8	11	5	4	19
Amp max	x	46	69	62	51	81
(kPa)	S.D.	19	12	21	6	26
	N	8	11	5	4	19
T10	x	343	287	1310	1064	766
(ms)	S.D.	311	116	512	634	373
	N	8	11	5	4	19
T90	x	73	103	339	266	241
(ms)	S.D.	56	60	239	226	164
	N	8	11	5	4	19
Tde	x	134	112	724	688	311
(ms)	S.D.	181	50	425	440	205
	N	8	11	5	4	19
Tin	x	140	68	233	115	218
(ms)	S.D.	203	40	208	82	207
	N	8	11	5	4	19

Pressure transducer alone

The T10, T90, Tde and Tin were the longest when the walrus sucked on the pressure transducer alone. The suction curves were quite irregular. An example is shown in figure 3C.

Fish in air

In each trial the animal usually sucked a few times without being able to move the fish. The final successful suck either pulled the entire fish from the trainer's hand, or the fish was pulled apart, leaving about half of it in the trainer's hand. In both events, the fish or a part of it was sucked over the sensor shortly after the suction was created. The values of the parameters measured during trials with herring and mackerel did not differ statistically, and therefore are analysed together.

Compared to the other test situations (except when the animal was sucking on the pressure transducer alone), the T90, Tde and Tin were on average long when the walrus sucked on fish in air. A typical example of a suction curve is shown in figure 3D.

Fish under water

The most conspicuous differences between under water and in-air suction on fish were the on average shorter T10 and Tde, the longer Tin and larger Amp 90 under water. The lines of the suction curves were smoother than when fish was sucked on in air. An example of a suction curve is shown in figure 3E.

Discussion

Physics

Fay (1982) reports on an anecdotal observation of a walrus which produced a pressure of around −91.4 kPa (−0.914 Bar) when sucking a tube which was connected to a mechanical pressure gauge. At the time of measurement, the animal was pulling air along the mouth piece. In the present study, using more sophisticated equipment, the lowest pressure recorded (Amp max) in air was −87.9 kPa (−0.879 Bar) when the walrus sucked on the pressure transducer. The minimum pressure reached while sucking under water was lower; −118.8 kPa (−1.188 Bar) when the walrus was sucking a mackerel.

The buccal cavity of a walrus can be regarded as a cylinder with a piston (the tongue). In rest, the tongue fills the buccal cavity almost entirely (Kastelein et al. 1991), so the initial volume of the cavity is practically zero. When the tongue is withdrawn to a caudal position, the volume of the buccal cavity is enlarged.

If the mouth cavity is filled with air, pressure (p) and mouth volume (V) are related by Boyle's law: $p_i \cdot V_i = p_f \cdot V_f$ (i = initial, f = final). As $V_f \gg V_i$ and p_i = the atmospheric pressure = 1 atm., it follows that p_f is close to 0 atm.; so the mouth cavity is close to vacuum. In air, the pressure cannot reach a value below 0 atm., so that a pressure transducer may record a pressure of maximally 1 atm. below the "baseline" of ambient pressure.

In water, the situation is different, and Boyle's law does not apply. When the piston is withdrawn to generate pressure of 0 atm., the water column will break after a certain short period and the cavity will be filled with water, water vapour and gas that was originally dissolved in the water. This phenomenon is unstable and is called "cavitation". At sufficiently low pressure, cavitation always occurs for a time, the length of which depends on the pressure and on the concentration of particles and dissolved gas in the water.

On a shorter time scale, the force applied to the piston may be transformed directly to

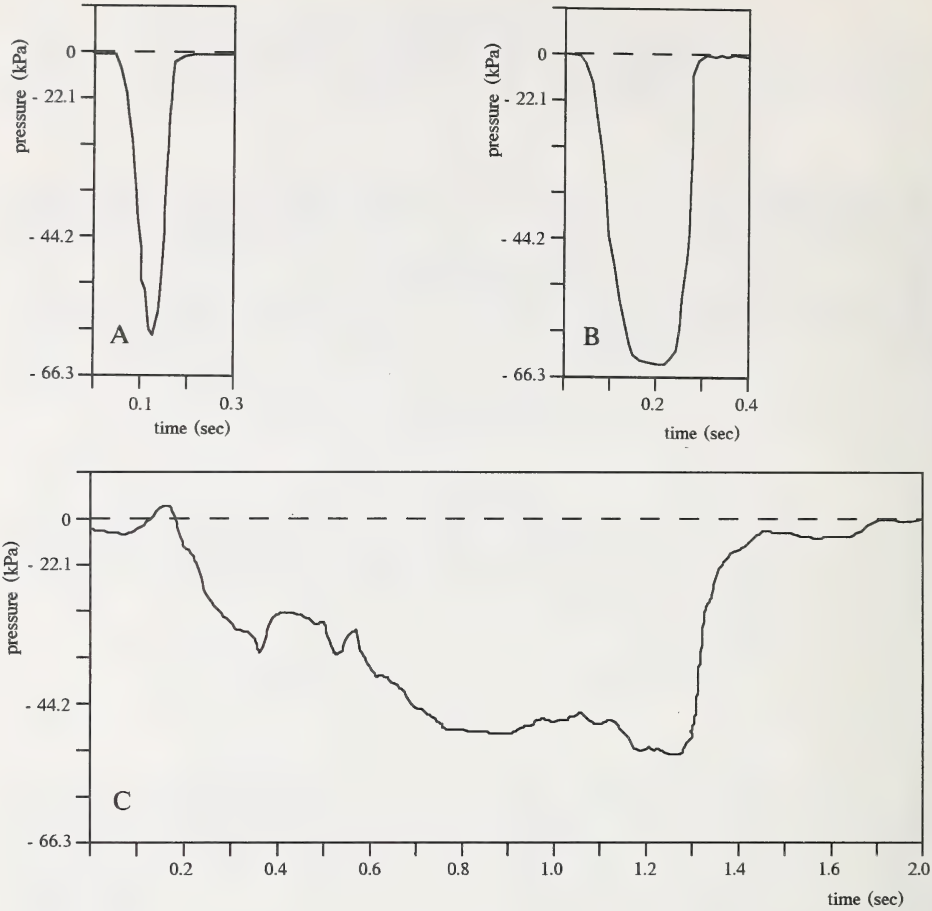

Fig. 3 A–C

pressure. So, a walrus may theoretically be able to generate a pressure of more than 1 atm. below ambient pressure for a short time.

In the above explanation, it is assumed that the flow through the mouth aperture is insignificant. In reality, food will be sucked into the oral cavity during tongue retraction and the pressure changes in the buccal cavity will be more complex.

Finger in air

The short T90 and small Amp90 are probably due to the fact that this was a trained behaviour in which the animal was rewarded for producing the "suction" sound, and not for the maximum suction power, or duration. From experience the animal probably knew it would not be able to suck in the object (= finger).

Cheek in air

The suction parameters between trials were rather similar when the animal sucked on a cheek in air. This is probably because other than the walrus' tongue, nothing moved into

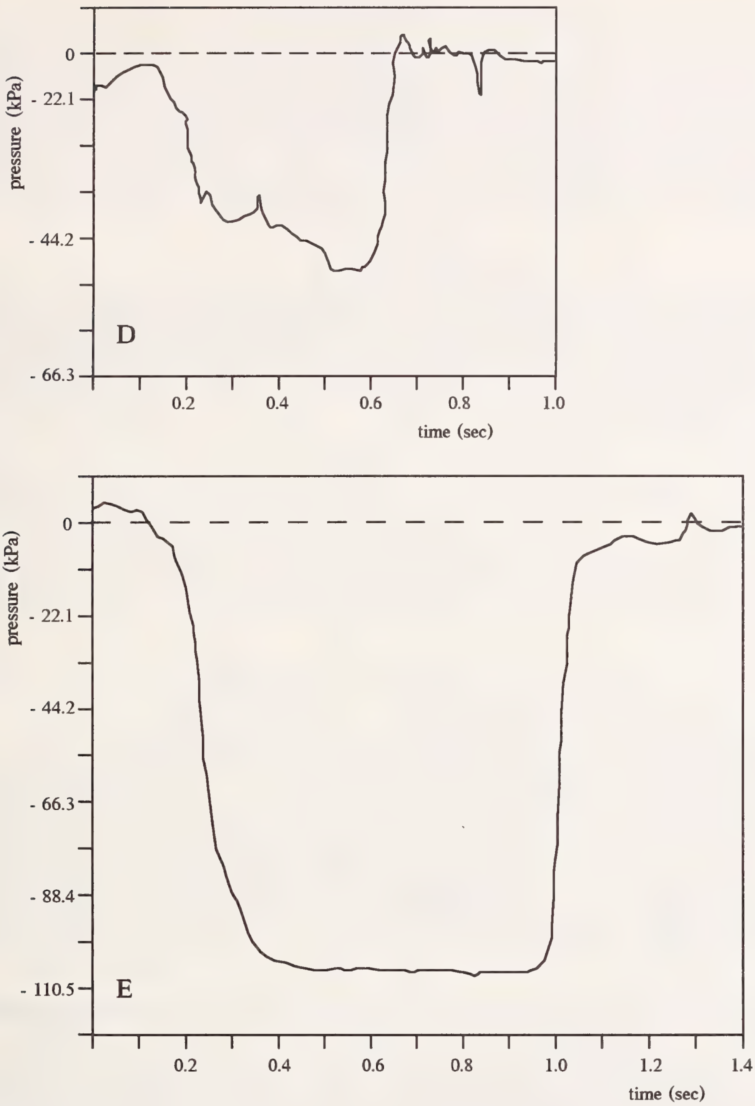

Fig. 3 (see also left side). Typical examples of suction curves on the same scales of time and pressure of A: Finger in air, B: Cheek in air, C: Pressure transducer alone, D: Fish in air, and E: Fish under water

the oral cavity and because the walrus controlled the entire situation. It started the trial by putting its lips against the cheek with a certain pressure, retracted its tongue, and allowed some air to enter the oral cavity to produce the "kiss" sound it was trained to produce in performances. The lips did not surround an object, but were pushed against the cheek of the trainer. This apparently also closed off the oral cavity tightly, resulting in a high Amp90. However, this parameter was not as high as when sucking fish under water. Air flows faster into the oral cavity than water, thus the pressure amplitudes in air are less negative than in water.

Pressure transducer alone in air

The long duration of the suction event when sucking the transducer alone in air can be explained by the fact that the transducer only filled a minute portion of the oral cavity, leaving a large volume of air to be expanded. This allowed the tongue to retract completely, which took more time. The relatively large Amp90 indicates that the walrus is able to close its lips tightly, even around such a small diameter pressure transducer. However, some air probably leaked into the oral cavity causing the irregularities in the suction curves.

Fish in air

The suction curves produced on fish in air are irregular. Pressure changes are probably caused by air leaking around the fish while it was sliding into the oral cavity. The suction events are long probably because the walrus attempted to swallow the fish. The irregularities at the end of the suction event in figure 3D are caused by the fish slipping over the pressure transducer.

Fish under water

During suction on fish under water the Tde was shorter, the Amp90 much higher, and the Tin longer than in air, probably because water flowed into the oral cavity more slowly than air. During the Tin the fish was pulled from the hand quickly and some water probably flowed into the oral cavity. The irregularity at the end of the suction event in figure 3E is caused by the fish slipping over the pressure transducer.

Correlations between suction parameters

To determine the level of control the walrus has over the different suction parameters, the correlations between these parameters were calculated. The correlations between the different suction curve parameters in all situations in air and under water are shown in table 2. The parameters within the following pairs are positively correlated both in air and under water: T10-Tde, T10-T90 and T10-Tin. This means that the longer the entire suction event (T10), the longer each of its 3 time components (Tde, T90 and Tin). Under water the parameters of the following 2 parameters pairs are positively correlated: Amp90-T90 and Tin-Tde. These are not correlated in air. This is probably due to the high density of water

Table 2. **The correlation between the different suction parameters in air (A) and under water (B)**
A – indicates no significant correlation. A + indicates significant correlation ($p < 0.05$)

A. Suction in air ($N = 29$, significance at $r > 0.306$)

	T10	T90	Tde	Tin
T90	+			
Tde	+	+		
Tin	+	+	–	
Amp90	–	–	–	+

B. Suction in water ($N = 17$, significance at $r > 0.412$)

	T10	T90	Tde	Tin
T90	+			
Tde	+	–		
Tin	+	–	+	
Amp90	–	+	–	–

compared to air. Water passes between the object and the lips with more difficulty, causing a higher force to retract the tongue which causes a slow sliding movement of the prey. In air, probably too much air leaks into the oral cavity, and the animal may not be able to maintain a large Amp90 for a long period without air leaking into the oral cavity. In air, the parameters of the following 2 pairs are positively correlated: Tde-T90 and Tin-T90. These are not correlated under water. This is probably due to the different shapes of the suction curves; in air, they are often V-shaped, while under water they are usually U-shaped.

Ecological significance

The present study shows that at least 3 parameters influence the shape of the suction curve (Tab. 3). The Tde is influenced by the retraction speed of the tongue, the tightness of the lips on the food item, and the presence of sealing mucus. The T90 is influenced by the time the animal can keep or decides to keep its tongue retracted, the tightness of the lips on the food item, and by the toughness and slipperiness of the food item and the strength of the trainer. The Amp90 is influenced by the strength and volume of the tongue, the initial position of the tongue in the buccal cavity, the fit of the tongue in the buccal cavity, the tightness of the lips around the food item and also by the shape, firmness and toughness of the food item and the presence of sealing mucus.

Table 3. **Parameters which influence the shape of the suction curve**

	Tde	T90	Amp90
Walrus	1. Retraction speed of tongue 2. Tightness of lips on food item	1. Time the animal can keep or decides to keep its tongue retracted 2. Tightness of lips on food item	1. Strength of tongue 2. Initial position of tongue 3. Fit of tongue in buccal cavity 4. Volume of tongue 5. Tightness of lips on food item
Food item	Sealing mucus	1. Toughness 2. Slipperiness	1. Shape 2. Firmness 3. Toughness 4. Sealing mucus
Trainer	-	Strength	

In air, the walrus normally uses its capacity for oral suction mainly during its suckling period. Ray (1960) describes a walrus calf which emptied a 225 ml baby bottle in 15 seconds, and often sucked the plastic container flat. Walruses have a relatively long suckling period of at least 15 months (Fay 1982), and suckling probably occurs both on land and under water (Miller and Boness 1983). Some walruses sometimes eat seals and use in air and under water oral suction to process their prey. Only strips of skin and blubber are found in walrus stomachs, indicating that these parts only are sucked off without mastication (Collins 1940; Breshin 1958; Perry 1967; Lowry and Fay 1984; Fay et al. 1990; Timoshenko and Popov 1990).

When a walrus encounters a clam in the sea bed, whether the clam will be eaten or not depends on the behaviour of both organisms. For the clam, its shape, firmness and toughness and the ability to detect a walrus are of importance. Shape and firmness are fixed properties of a clam, but the toughness of the siphon may depend on its retraction state. The more retracted, the more difficult it is to suck the clam out of its shell. For the walrus

the volume, strength and retraction speed of the tongue and the firmness of the lips on a food item are of importance. The volume seems to be a fixed property, unless the walrus can retract the tongue partly during a suction event. The walrus can probably determine the strength and retraction speed of its tongue and the pressure on the clam with its lips. The pressure of the funnel-shaped lips should be sufficient to prevent water from flowing around the prey into the oral cavity, but low enough to prevent the clam's shells from breaking. Depending on the toughness of its prey, the walrus may retract its tongue faster, or use more muscle bundles. Possibly, the walrus has an expectation of the toughness of its prey before it sucks. If that is true, the Tde is mainly consciously determined by the walrus. This explains also part of the correlations in table 2. If a siphon is slowly stretched during a suck, the toughness is slowly decreased until the siphon breaks off the clam's body. This might explain the function of the long T90's found in the present study (in air 625 ms and under water 658 ms); because the walrus was eager to swallow the fish, she kept her tongue retracted for a longer time.

The present study provides insight into the control a walrus has over its oral suction power, speed and duration. Whether the walrus can process bivalve molluscs at all stages of siphon and foot retraction remains to be determined.

Acknowledgements

We thank trainer Piet Mosterd for his practical help with the experiment, Dr. Bernhard Neurohr (Duisburger Zoo) for translation of the summary, and Prof. Jan Osse and Prof. Piet Wiepkema (Agricultural University of Wageningen), and Nancy Vaughan for their comments on the manuscript.

Zusammenfassung

Orales Saugvermögen eines Pazifischen Walrosses (Odobenus rosmarus divergens) in Luft und unter Wasser

Walrosse fressen hauptsächlich sessilen tierischen Benthos. Von zweischaligen Weichtieren werden normalerweise nur die Siphonen und Füße in Walroßmägen gefunden. Es wird allgemein angenommen, daß Walrosse durch ihr Saugvermögen Weichtiere von deren Schalen trennen können. In der Mundhöhle kann Unterdruck dadurch erzeugt werden, daß die wie ein Kolben funktionierende Zunge zurück- und heruntergezogen wird. Während mehrerer Über- und Unterwasser-Saugtests wurde der Druck in der Mundhöhle einer Walroßkuh gemessen. Durch Saugen am Druckübermittler konnte über Wasser als niedrigster Druck – 87,9 kPa (−0,879 bar; fast Vakuum) gemessen werden. Beim Ansaugen einer Makrele unter Wasser konnte als niedrigster Druck −118,8 kPa (−1,188 bar) registriert werden. Da das Walroß seine Zungenmuskeln präzise kontrollieren kann, sind Druck und Dauer des Saugaktes gut regulierbar.

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Authors' addresses: Ron A. Kastelein, Harderwijk Marine Mammal Park, Strandboulevard-oost 1, NL-3841 AB Harderwijk, Holland; Mees Muller and Arie Terlouw, Department of Experimental Animal Morphology and Cell Biology, Agricultural University, Zodiac, Marijkeweg 40, NL-6709 PG Wageningen, Holland

Z. Säugetierkunde 59 (1994) 116–125

ISSN 0044-3468

Comparative morphometry and cytogenetics of *Microtus (Terricola) multiplex* (Arvicolidae, Rodentia) of the western French Alps

By P. Brunet-Lecomte and V. Volobouev

Centre des Sciences de la Terre, Université de Bourgogne, Dijon, France and Institut Curie, Paris, France

Receipt of Ms. 25. 11. 1991
Acceptance of Ms. 11. 2. 1993

Abstract

The western French Alpine populations of *Microtus (Terricola) multiplex* (Arvicolidae, Rodentia) occupy the marginal distributional area of the species. Analysis of the characters of the Relative Length of the Anterior Part (RLAP) and of the Pitymyan Rhombus (PR) of the first lower molar (M_1) of these populations and subsequent comparison with other populations from the Central Alps of France and Switzerland permits to distinguish the populations of the western French Alpine area (Saint-Martin-de-la-Cluze and La-Chapelle-en-Vercors) from the populations of the Central Alps belonging to the subspecies *multiplex, fatioi* and *druentius*. Karyological analysis of the population from Saint-Martin-de-la-Cluze confirms the cytogenetic differentiation of populations from the western French Alpine area which are characterized by a subtelocentric X chromosome and a metacentric Y chromosome. The synthesis of these results leads to the proposal of a new subspecies for the populations from the western French Alpine area, *Microtus (Terricola) multiplex niethammeri* nov. ssp.

Introduction

European ground-voles of the subgenus *Terricola* constitute an advantageous group for study of speciation because of their geographic chromosomal variation (Meylan 1970, 1972; Winking 1976; Storch and Winking 1977; Graf and Meylan 1980) and their discontinuous distribution (Niethammer and Krapp 1982). The Alpine ground-vole *M. (T.) multiplex* (Fatio 1905), a species of the Middle European phyletic group (Brunet-Lecomte 1990) is characterized by chromosomal polymorphism of 2n = 46 to 48 and NF = 52 to 54 (Niethammer and Krapp 1982). Since the species was first described by Fatio in 1905, six subspecies have been identified: *multiplex* (Fatio 1905) from Lugano (Ticino, Switzerland), *fatioi* (Mottaz 1990) from Zermatt (Wallis, Switzerland), *druentius* (in Miller 1912) from Terres-Plaines near Barcelonnette (Alpes-de-Haute-Provence, France), *orientalis* (Dal Piaz 1924) from Madonna di Campiglio (Trentino, Italy), *liechtensteini* (Wettstein-Westersheim 1927) from the top of Mali Rainac mountain near Krasno (Croatia, Yugoslavia), *petrovi* (Krystufek 1983) from Socerga near Koper (Slovenia, Yugoslavia). In France the species occurs in the southern Central Alps (Mercantour, Ubaye, Briançonnais), northern Central Alps (Vanoise), western Pre-Alps (Vercors, Chartreuse) and perhaps further west as far as the Rhone Valley and eastern Massif Central (Heim de Balsac and Beaufort 1966; Brosset and Heim de Balsac 1967; Niethammer and Krapp 1982; Fayard 1984). Cytogenetic and electrophoretic studies of the western and Central Alpine subspecies *multiplex, fatioi* and *druentius* (Graf and Meylan 1980) underline the differentiation of the population of La-Chapelle-en-Vercors from the western Pre-Alps of Vercors (Tab. 1). This population is characterized by a subtelocentric X chromosome (Graf and Meylan 1980) and a high genetic distance of Nei in comparison with the other studied populations (between 0.09 and 0.18) (Graf and Meylan 1980),

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Table 1. **Chromosome data of *Microtus (Terricola) multiplex***

Locality	2n	FN	Karyotype Autosomes	X	Y	References
1 Gudo (E), Meride (F), Varenzo (H), Zermatt (I)	48	50	2 lST + 2 mM + 42 A	SM	A	Graf and Meylan (1980)
2 La Cayolle (J) Le Lautaret (C)	48	50	2 lST + 2 mM + 42 A	SM	M*	Graf and Meylan (1980)
3 La-Chapelle-en en-Vercors (B)	48	50	2 lST + 2 mM + 42 A	ST	A	Graf and Meylan (1980)
4 Saint-Martin de la-Cluze (A)	48	50	2 lST + 2 mM + 42 A	ST	M	present study
5 Fivizzano (L)	46	48	2 lST + 2 mM + 40 A	SM	A	Graf and Meylan (1980)
6 Arsié (M)	46	46	2 lA + 2 mM + 40 A	lSM	lA	Storch and Winking (1977)
7 Calliano (N)	46	46	2 lA + 2 mM + 40 A	lSM	lSM	Storch and Winking (1977)

Locality: letters in brackets denote the labels of populations from figure 1. Karyotype: A = acrocentric, ST = subtelocentric, SM = submetacentric, M = metacentric, m = medium, l = large. *: although the authors suggest that the unpaired medium-sized metacentric may be the Y chromosome, definitive interpretation is made by us.

corresponding to an inter-subspecies distance, whereas the genetic distances calculated between the populations from Ticino (subspecies *multiplex*), Zermatt (subspecies *fatioi*) and Briançonnais (subspecies *druentius*) are smaller (between 0.02 and 0.06).

The aim of this study is to present the karyotype of a population of *M. (T.) multiplex* from Saint-Martin-de-la-Cluze, in the Drac Valley, which lies near, although outside, the Pre-Alps of the Vercors; to compare the karyotype and the first lower molar morphology of this population with those of the other populations of the Alps and to clarify the systematics of the populations from the western French Alpine area.

Material and methods

Nine populations were studied, each presented by 10 teeth (M_1). The populations were from: A: Saint-Martin-de-la-Cluze (Isère, France); B: La-Chapelle-en-Vercors (Drôme, France); C: Col du Lautaret (Hautes-Alpes, France); D: Les Vigneaux (Hautes-Alpes, France); E: Gudo (Ticino, Switzerland); F: Meride (Ticino, Switzerland); G: Bioggio (Ticino, Switzerland); H: Varenzo (Ticino, Switzerland); I: Zermatt (Wallis, Switzerland).

Localities are mapped in figure 1.

Morphology of the first lower molar (M_1)

The analysis of the characters Relative Length of the Anterior Part (RLAP) and Pytymyan Rhombus (PR) was based on the comparison of means between the populations according to the analysis of variance method completed by Scheffé's method.

Chromosomal study

Chromosome preparations were obtained from primary fibroblast cultures from tail biopsies of four specimens (2♂♂ and 2♀♀) all from Saint-Martin-de-la-Cluze (Isère, France). Explants and a portion of the cells of studied specimens are routinely kept in liquid nitrogen in the cell and tissue collection of the Laboratoire de Structure et Mutagenèse Chromosomiques (Institut Curie, Paris, France).

Fig. 1. Localities of the populations studied. M o r p h o l o g i c a l s t u d y. A: Saint-Martin-de-la-Cluze (Isère, France); B: La-Chapelle-en-Vercors (Drôme, France); C: Col du Lautaret (Hautes-Alpes, France); D: Les Vigneaux (Hautes-Alpes, France); E: Gudo (Ticino, Switzerland); F: Meride (Ticino, Switzerland); G: Bioggio (Ticino, Switzerland); H: Varenzo (Ticino, Switzerland); I: Zermatt (Wallis, Switzerland). K a r y o l o g i c a l s t u d y. A; B; C; E; F; H; I; J: Col de la Cayolle (Alpes-de-Haute-Provence, France); L: Fivizzano (Toscana, Italy); M: Arsie (Italy); N: Calliano (Italy).
T y p e l o c a l i t i e s : O: Lugano (Ticino, Switzerland) = *multiplex*; I = *fatioi*; K: Terres-Plaines near Barcelonnette (Alpes-de-Haute-Provence, France) = *druentius*; P: Madonna di Campiglio (Trintino, Italy) = *orientalis*; Q: Top of Mali Rainac mountain near Krasno (Croatia, Yugoslavia) = *liechtensteini*; R: Socerga near Koper (Slovenia, Yugoslavia) = *petrovi*.
H a t c h i n g : the Alps

Mitotic chromosomes were studied with RHG R-banding and CBG C-banding (Harnden and Klinger 1985) after, Carpentier et al. (1972) and Summer (1972) respectively. Replication banding (RBG) was studied using the method of Viegas-Péquignot and Dutrillaux (1978). At least 20 metaphase plates were analysed for each specimen.

Results

Morphological analysis of M_1 characters

a. RLAP: The mean and the standard deviation of the RLAP of each population are given in table 2. The distribution of means of each population is given in figure 2. The RLAP is significantly less developed in the populations A and B (Saint-Martin-de-la-Cluze and La-Chapelle-en-Vercors) than in the populations C and D (Briançonnais) and E to H (Ticino); population I (Zermatt) having an intermediate RLAP between those of these populations.
b. PR: The mean and the standard deviation of the PR of each population are given in table 3. The distribution of means of each population is given in figure 3. The PR is significantly greater (less inclined) in the populations C and D (Briançonnais) than in the other populations.

Chromosomal study

Karyotypes of all four specimens from Saint-Martin-de-la-Cluze are similar and characterized by 2n = 48 and FN = 54. All pairs of autosomes and both sex chromosomes were precisely identified by high resolution R-banding (Fig. 4). Among autosomes two pairs are biarmed, one of them, the largest in the karyotype, is subtelocentric, while the other N° 6 is a medium sized metacentric. The X chromosome is subtelocentric and similar in size to

Table 2. **Mean and standard deviation (SD) of the Relative Length of the Anterior Part (RLAP) of the M_1 (no units)**

Analysis of variance and Scheffé's test. Populations (Pop.) A–I as shown in figure 1

Pop.	N	Mean	SD	Group	N	Mean	SD	Scheffé's test*	
A	10	0.507	0.019						
B	10	0.503	0.025	A and B	20	0.505	0.021	1	
C	10	0.518	0.025						
D	10	0.528	0.014	C and D	20	0.523	0.020		2
E	10	0.525	0.011						
F	10	0.521	0.013						
G	10	0.521	0.012	E to H	40	0.523	0.012		2
H	10	0.525	0.012						
I	10	0.513	0.015	I	10	0.513	0.015	1	2
					Analysis of variance		$p = 0.0007$		

* Means with the same number are not significantly different.

Table 3. **Mean and standard deviation (SD) of the Pitymyan Rhombus (PR) of the M_1**

Analysis of variance and Scheffé's test. Populations (Pop.) A–I as shown in figure 1 (unit 10^{-2} mm)

Pop.	N	Mean	SD	Group	N	Mean	SD	Scheffé's test*	
A	10	1.40	3.47						
B	10	−0.30	2.58	A and B	20	0.55	3.10	1	
C	10	10.40	3.57						
D	10	4.80	5.27	C and D	20	7.60	5.24		2
E	10	2.90	2.38						
F	10	0.70	2.98						
G	10	4.80	3.29	E to H	40	3.55	3.33	1	
H	10	5.80	2.39						
I	10	2.10	3.31	I	10	2.10	3.31	1	
					Analysis of variance		$p < 0.0001$		

* Means with the same number are not significantly different.

the largest acrocentric pair, the Y chromosome is metacentric and similar in size to 14–15th pairs of autosomes. C-banding analysis (Fig. 5) revealed that all the autosomes possess a small centromeric block of C-heterochromatin. The Y chromosome is almost entirely C-positive. The short arms of the X chromosomes are late replicating and thus heterochromatic (Fig. 4) although C-heterochromatin was detected in their proximal parts (Fig. 5). No obvious variation of C-heterochromatin was noticed either among the cells or among the animals studied.

Discussion

The analysis of the characters RLAP and PR shows that populations A and B (Saint-Martin-de-la-Cluze and La-Chapelle-en-Vercors) can be clearly distinguished, on the one hand, from populations C and D (Briançonnais) of the inner French Alps by their more steeply inclined PR and by their less developed RLAP, and on the other hand, from populations E to H of Ticino by their less developed RLAP. This same analysis of characters shows that populations A and B are close to population I of Zermatt (Wallis) despite the geographical isolation of this latter population (Graf and Meylan 1980). In comparison with other existant European species, *Microtus (Terricola) multiplex* is charac-

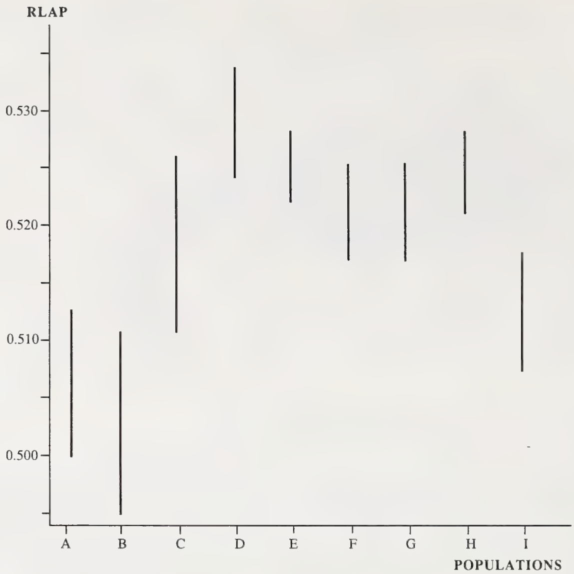

Fig. 2. Distribution of the mean +/− standard error of the mean of the Relative Length of the Anterior Part (RLAP) of the M_1. For populations' A–I distribution see figure 1 (no units)

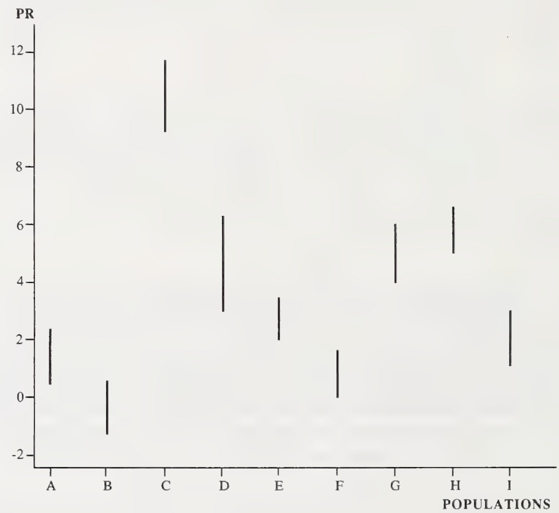

Fig. 3. Distribution of the mean +/− standard error of the mean of the Pitymyan Rhombus (PR) of the M_1. For populations' A–I distribution see figure 1 (unit 10^{-2} mm)

terized by a poorly inclined PR (Brunet-Lecomte 1990). Therefore the inclined PR of populations A and B leads us to believe that the populations from the western French Alps are derived from a Central Alpine subspecies (*druentius* or *multiplex*).

Microtus (Terricola) multiplex has been relatively well studied karyologically: to date, at least 25 populations have been studied over most of its distributional area (see Zima and Kral 1984; Zagorodnyuk 1990). The published data show that all cases of chromosomal

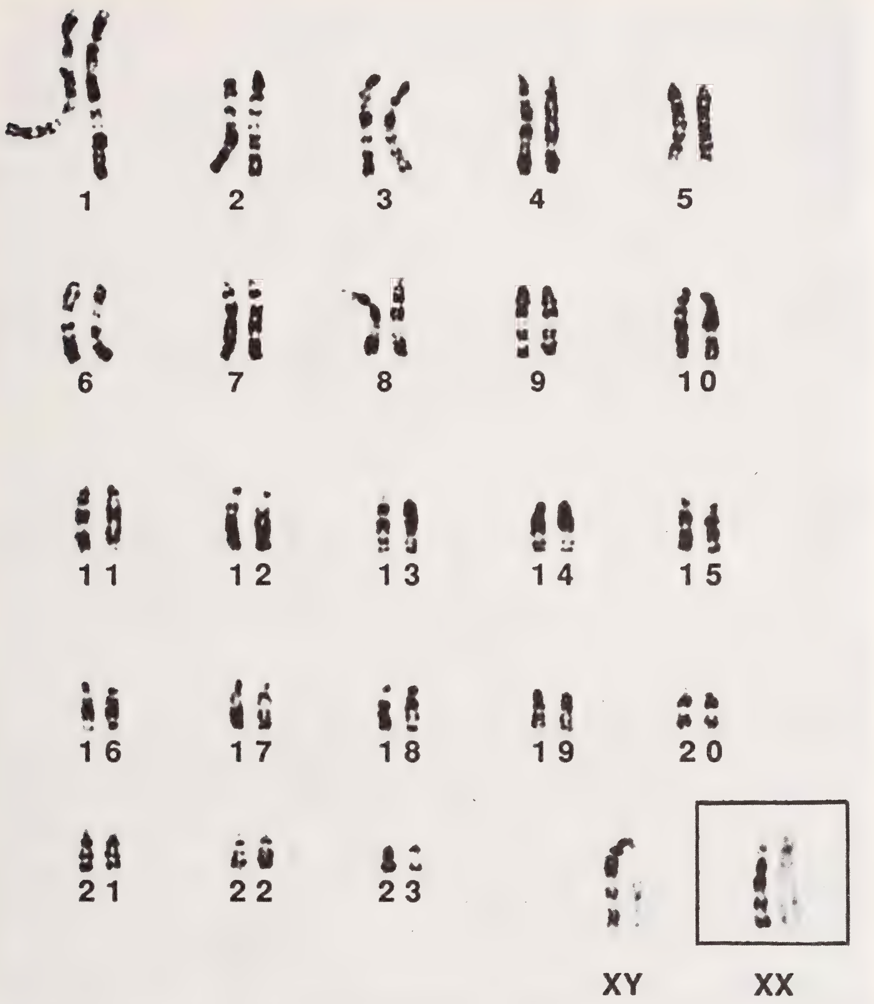

Fig. 4. R-banded (RBG) chromosomes of *Microtus (Terricola) multiplex*. Female sex chromosomes are given in the insert. One of the X chromosomes and both short arms are late replicating

variation but one (see below) have been observed between populations, thus, pointing to chromosomal polytypy and not chromosomal polymorphism. All known chromosome forms including the new one from Saint-Martin-de-la-Cluze are presented in table 1. As can be seen from these data, there are two types of karyotypes among these forms, with 46 and 48 chromosomes. The Italian karyotypic forms with 2n = 46 are different from each other. The form from Fivizzano (Graf and Meylan 1980) differs from the 48 chromosome forms by the loss of a pair of acrocentric autosomes, while the sex chromosomes are similar to those in form 1 (Tab. 1). The next two forms with 2n = 46 (differing from each other by morphology of the Y chromosome) both belong to subspecies *liechtensteini* and are different from all 48 chromosome forms, as well as that with 2n = 46 from Fivizzano. These differences concist in a translocation of both sex chromosomes into a pair of large

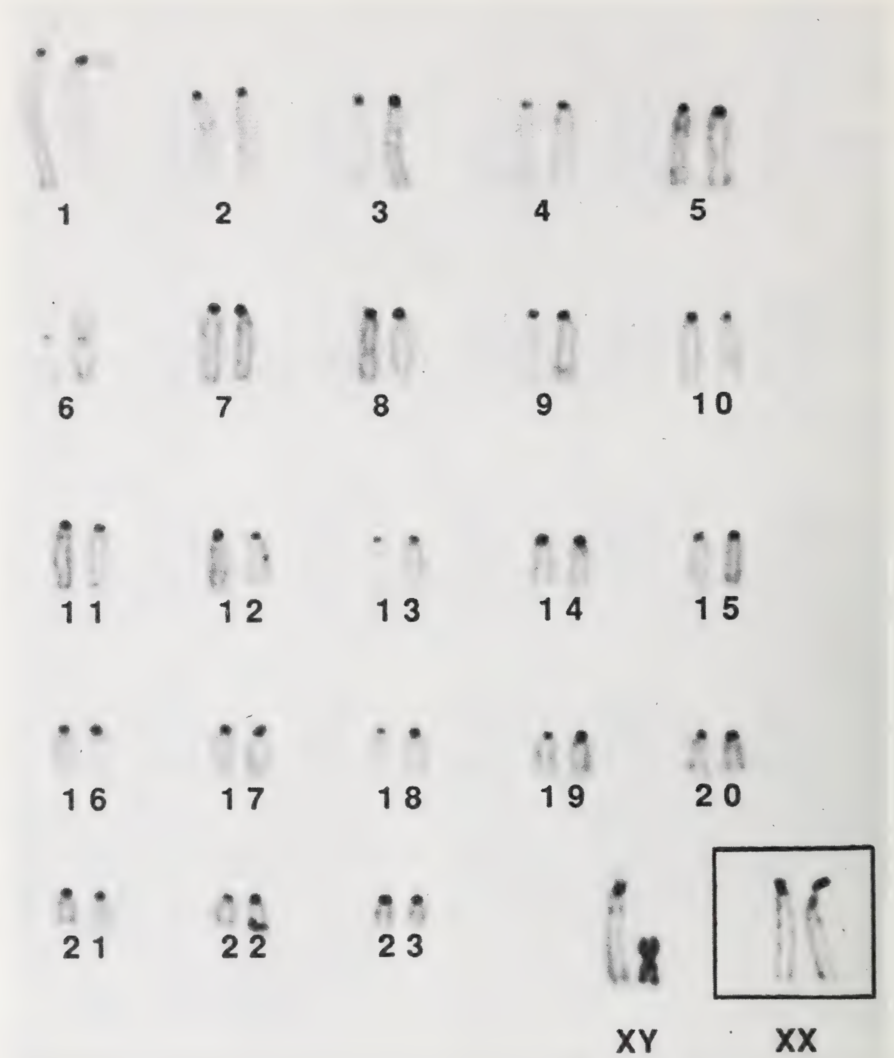

Fig. 5. C-banded chromosomes of *Microtus (Terricola) multiplex*. The sex chromosomes of a female are given in the insert

acrocentric autosomes, and an acrocentric state of the largest pair of autosomes in comparison with a submetacentric state in all other forms and the presence of an additional subtelocentric pair of autosomes. In our opinion these rearrangements are sufficient to ensure cytogenetic isolation of this form, and we subscribe to Petrov and Zivkovic's (1971) conclusion that *liechtensteini* is a distinct species although this was queried in subsequent studies (Storch and Winking 1977; Graf and Meylan 1980; Zagorodnyuk 1990). The differences between karyotypic forms with 2n = 48 are caused by different morphology of the sex chromosomes. Therefore, the X chromosome may be submetacentric or subtelocentric and the Y chromosome acrocentric or metacentric. All four possible combinations of different variants of the X and the Y chromosomes are found in nature,

always in different populations. The only exception is a female heterozygous specimen featuring submetacentric and subtelocentric variants of the X chromosome. It was collected in a population of Briançonnais not far from the population of La-Chapelle-en-Vercors (Tab. 1) and was probably of hybrid origin (GRAF and MEYLAN 1980).

The karyological differences between 48 chromosome forms are hardly capable of providing cytogenetic isolation by themselves but they might serve as indications as to the level of differentiation and origin of the chromosome forms. Therefore, the occurrence of the same variant of the X chromosome in two neighbouring populations of *M. (T.) multiplex* (Saint-Martin-de-la-Cluze and La-Chapelle-en-Vercors) not found elsewhere undoubtedly means they have a common origin. The close relationships between these populations also follow from morphological analysis of M_1. On the other hand, the population of La-Chapelle-en-Vercors is genetically more distant from all the other studied populations (GRAF and MEYLAN 1980). These observations are in agreement with paleontological data on the isolation of western Alpine populations of *M. (T.) multiplex* during the Upper Pleistocene cited by GRAF and MEYLAN (1980).

Thus, the data provide new evidence concerning the particular taxonomic position of populations in the western French Alps.

The karyological, genetical and morphometrical analyses made by GRAF and MEYLAN (1980) and our research lead to the following conclusion: the populations from Saint-Martin-de-la-Cluze and La-Chapelle-en-Vercors are sufficiently differentiated to be classified as belonging to at least a new subspecies.

Microtus (Terricola) multiplex niethammeri nov. ssp.

Holotype: Adult male (skin and skull), Centre des Sciences de la Terre de l'Université de Bourgogne N° DIMMUL891001.

Type locality: Saint-Martin-de-la-Cluze, Isère, Rhône-Alpes, France.

Diagnosis: Subspecies characterized by the following karyotype: Autosomes: 2 large subtelocentrics, 2 medium metacentrics, 42 acrocentrics; X chromosome: subtelocentric, Y chromosome: metacentric.

Morphological diagnosis of M_1: RLAP not very well-developed for the species *Microtus (Terricola) multiplex*: mean +/− standard error of the mean = 0.507 +/− 0.006 (no units). PR inclined for the species *Microtus (Terricola) multiplex*: mean +/− standard error of the mean = 1.40 +/− 1.1 (unit 10^{-2} mm).

Distribution: Known from Saint-Martin-de-la-Cluze. The population from La-Chapelle-en-Vercors which differs by its Y acrocentric chromosome can be include in this subspecies.

Etymology: In honour of Prof. Dr. Jochen NIETHAMMER, Bonn, for his work on European voles.

Acknowledgements

We are indebted to F. CATZEFLIS and A. NADACHOWSKI for helpful comments and suggestions, to T. VOGEL and V. PARISOT for translation, to J. D. GRAF, A. MEYLAN, L. DE ROGUIN and M. SALVIONI for the loan of the M_1 from La-Chapelle-en-Vercors, Gudo, Meride, Bioggio, Varenzo, Zermatt; to F. SPITZ for the loan of the M_1 from Col du Lautaret and Les Vigneaux; to J. F. CONSTANT for the help in trapping voles at Saint-Martin-de-la-Cluze.

This research was supported by the French C.N.R.S.: Programme "Modalités évolutives" de l'URA 157 and A.S.P. "Evolution" as well as "Approches interdisciplinaires et développements méthodologiques" de la Direction de la Recherche et des Etudes Doctorales, grant n° EU 1969 (resp. J. CHALINE).

Résumé

Morphométrie et cytogénétique comparées de Microtus (Terricola) multiplex (Arvicolidae, Rodentia) des Alpes occidentales françaises

Les populations de la partie occidentale des Alpes françaises de *Microtus (Terricola) multiplex* (Arvicolidae, Rodentia) occupent une position marginale dans l'aire de distribution de l'espèce. La comparaison des caractères longueur relative de la partie antérieure et rhombe pitymyen permet de séparer les populations de la partie occidentale des Alpes françaises des autres populations des Alpes internes. L'analyse cytogénétique de la population de Saint-Martin-de-la-Cluze (Isère, France) confirme la différenciation chromosomique des populations de la partie occidentale des Alpes françaises, lesquelles sont caractérisées par un chromosome X subtélocentriqueet un chromosome Y métacentrique. La synthèse de ces résultats et de ceux de la littérature conduit à proposer une sous-espèce nouvelle pour les populations de la partie occidentale des Alpes françaises, *Microtus (Terricola) multiplex niethammeri* nov. ssp.

Zusammenfassung

Morphometrie und Cytogenetik von Microtus (Terricola) multiplex (Arvicolidae, Rodentia) der westlichen französischen Alpen im Vergleich

Die Populationen von *Microtus (Terricola) multiplex* (Arvicolidae, Rodentia) im westlichen Teil der französischen Alpen nehmen eine Randposition bei der räumlichen Verteilung der Art ein. Der Vergleich der Merkmale relative Länge des Vorderteils des M_1 und Pitymys-Rhombus am M_1 erlaubt eine Abtrennung der Populationen des westlichen Teils der französischen Alpen von den Populationen der inneren Alpen. Die Analyse der Chromosomensätze der Population von Saint-Martin-de-la-Cluze (Isère, France) bestätigt die chromosomale Differenzierung der Populationen des westlichen Teils der französischen Alpen, die gekennzeichnet sind durch ein subtelozentrisches X-Chromosom und ein metazentrisches Y-Chromosom. Diese Ergebnisse und die aus der Literatur führen zu dem Vorschlag einer neuen Unterart in den Populationen des westlichen Teils der französischen Alpen: *Microtus (Terricola) multiplex niethammeri* nov. ssp.

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Authors' addresses: Patrick Brunet-Lecomte, Centre de paléontologie analytique et géologie sédimentaire, URA CNRS 157, Laboratoire de préhistoire et paléoécologie du Quaternaire de l'EPHE, Centre des sciences de la terre, 6 Bd Gabriel, F-21000 Dijon, France and Vitaly Volobouev, Institut Curie, Structure et mutagenèse chromosomiques, URA CNRS 620, 26 rue d'Ulm, F-75321 Paris Cedex 05, France

Z. Säugetierkunde 59 (1994) 126–128

ISSN 0044-3468

WISSENSCHAFTLICHE KURZMITTEILUNG

Use of dung piles by neighbouring vicuñas

By Bibiana L. Vilá

Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Oxford, United Kingdom

Receipt of Ms. 9. 2. 1993
Acceptance of Ms. 1. 10. 1993

Dung-piling behaviour is typical among the South American camelids, and is notable in the wild vicuña (*Vicugna vicugna*) where both males and females, adults and young urinate and defecate in dung piles. Vicuña social organization is based upon stable family groups that live in an area defended year round, and bachelor groups which are more variable in composition and location. Bachelors and "passing vicuñas" usually use dung piles in family territories if the family is absent (drinking water or walking) (Koford 1957; Franklin 1974, 1980, 1983; Bosch 1984) suggesting that the marks "keep insiders in" instead of "keeping outsiders out". The aim of this study is to analyse the use of dung piles between adjacent families.

This study was conducted at the Abrapampa Experimental Station of the National Institute of Agricultural Tecnology (INTA). The station is located in dry grassland 3475 m above sea level in the Puna region of Jujuy Province, NW Argentina. For details of the study area see Vilá (1992). The vicuña stock of the station consisted of 600 animals living in a 400 ha area limited by sheep fence, containing natural pasture with a narrow river flowing through the area. No management techniques were used on these animals. The field work was carried out during March 1989. Observations were made from an observatory hut (6.5 m high) with binoculars.

The 16 dung piles that were located close to the observation hut were numbered. They were under view simultaneously (Fig.). The vicuñas belonging to the three families that use this area intensively were recognized individually. These families were: "NCla" with composition 1:3:1 (male:female:offspring), "Gde" 1:7:5 and "Mar" 1:4:2. When an animal (member of these families, member of a bachelor group, or solo) used a dung pile, a record was made of his/her identity and the individual number of the pile used. "Use" was considered when the animal defecated and/or urinated in the pile and not when they only smelled the pile.

In this study, vicuñas' behaviour in relation to the dung pile prior to elimination (smelling, kneading, turning and positioning) was the same as that described for the species in Perú (Koford 1957; Franklin 1980).

Use of dung piles: 140 defecation-urination events were observed. For each dung pile, the percentage of use by animals belonging to each family or no family groups and/or solo animals was calculated (Table). As is clear from the table, some dung piles were used exclusively by some families, while others were shared between families. The Figure shows the distribution of the dung piles and the location of families which used them. In almost all cases animals not belonging to these families made use of the piles. Among members of the family groups, males used the dung piles more than three times as often as females (t test 3.16 $p < 0.05$).

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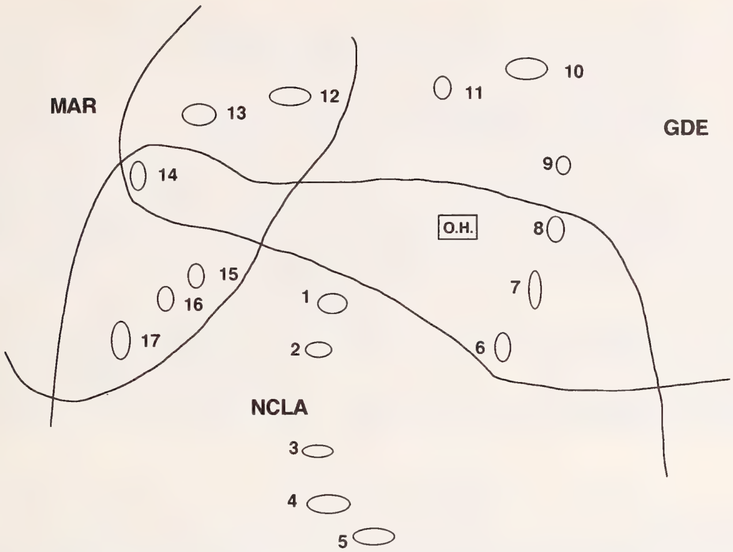

Distribution of the dung piles under observation and the families which shared them. The observation hut is marked as O. H.

Vicuñas territorial behaviour has been described as having very rigid boundaries, and the mating system has been described as "resource defence polygyny". (Franklin 1974, 1983). Some evidence of males defending females and retaining them in their territories has been found (Bosch 1984; Bosch and Svendsen 1987; Vilá 1990) (suggesting in Abrapampa a mixed mating pattern of territory and females defence, Vilá 1992) and also social organization has been found to differ according to wet/dry conditions, pasture and season (Menard 1982; Franklin 1983; Vilá and Roig 1992).

This study showed that although families used an area almost exclusively there was some tolerance between neighbours, and adjacent families used border areas at different

Percentage use of dung piles by animals belonging to different families and non-familiar ones

		Families		
Dung pile	NCLA	GDE	MAR	No-families
1	100 %			
2	87.5 %			12.5 %
3	75 %			25 %
4	75 %			25 %
6	40 %	40 %		20 %
7	66.6 %	16.6 %		16.6 %
8	11.1 %	77.8 %		11.1 %
9		71.4 %		28.6 %
10		64.3 %		35.7 %
11		100 %		
12		43.7 %	50 %	6.3 %
13				100 %
14	33.3 %	33.3 %		33.3 %
15	75 %			25 %
16	33.3 %		33.3 %	33.3 %
17	44.4 %		33.3 %	22.2 %
18	23 %		46.3 %	30.7 %

times. This territory overlap allowed one family to use the dung piles of another family. Koford (1957) showed that vicuñas used the nearest dung pile to defecate, and this might explain the pattern found here. In a study which analysed the relationship between scent marking and resource holding of some antelopes, Gosling (1990) discussed the possible function of scent-marking as status advertisement, reducing the cost of agonistic encounters. This hypothesis requires that males have to be "sufficientely sedentary" (Gosling 1990), which is the case in the vicuñas year-round defended areas. The scentmark as part of a compound (dung pile-male) causes bachelors to move out of the zone. The frequent use of the piles on the boundaries may mark the "possibilities" of expanding the territory (Gosling 1987), that is the tolerance male vicuñas have with their neighbours. This hypothesis can also explain why in the absence of the territorial male and the family, other animals use the piles; again the scentmark and the scent-marker form a compound and without both components the message is not the same. Thus, the data presented here are consistent with both "using the nearest" and "compound dung-pile/male" explanations.

Although preliminary, this work shows how a knowledge of the individual animals can help to discover differences in relation to previous information.

Acknowledgements

Many thanks to Ing. Jorge Bertoni, Director of the INTA-Abrapampa. This study was written while visiting the Wildlife Conservation Research Unit, University of Oxford, as a post-doctoral academic visitor supported by an external grant of the Argentine Research Council (CONICET) and British Council/Antorchas Fellowship. I thank Dr. David Macdonald, head of the "Wildcru". Dr. Rosie Woodroffe corrected the English. I am very grateful to Dr. Marcelo Cassini for his criticism and help with this work.

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Author's address: Dr. Bibiana L. Vilá, GEMA-Sur, Estanislao del Campo 1260, (1602) Florida, Pcia. de Buenos Aires, Argentina

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Z. Säugetierkunde 59 (1994) 2, 65–128

Vol. 59 (3), 129–192, Juli 1994 ISSN 0044-3468 C 21274 F

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde

Verlag Paul Parey Hamburg

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 Verlag: Paul Parey GmbH & Co. KG, Hamburg. Anschrift: Spitalerstr. 12, D-20095 Hamburg, Bundesrepublik Deutschland.
Printed in Germany by Westholsteinische Verlagsdruckerei Boyens & Co., Heide/Holst.

Z. Säugetierkunde 59 (1994) 129–138

ISSN 0044-3468

Territorial marking in the Yellow mongoose *Cynictis penicillata*: sexual advertisement for subordinates?

By BRIGITTE A. WENHOLD and O. ANNE E. RASA

Department of Zoology, University of Pretoria, Pretoria, RSA and Zoologisches Institut, Universität Bonn, Bonn, FRG

Receipt of Ms. 24. 9. 1993
Acceptance of Ms. 25. 2. 1994

Abstract

In the yellow mongoose, a colonial territorial viverrid, territory marking is performed by all group members. Subordinate adults, both male and female, have higher marking rates than the dominants and juveniles of both sexes and their marks carrying identity cues are deposited especially in border areas and outside the territory. They are also the animals most involved in territorial defence. Within the territory, marking was concentrated around the burrow systems and dominants either did not mark (dominant male) or did not visit (dominant female) the territory borders. Subordinate males, which have low reproductive success in their natal colonies, disperse usually to neighbouring colonies and subordinate females cross territory borders when in oestrus and are mated by males from neighbouring groups. The classes of animal most likely to seek mating opportunities outside the colony thus mark most often where their marks will be encountered by strangers. Apart from its role in territory familiarisation and territory owner assessment, marking in this species is hypothesised as being a means of sexual advertisement for subordinate animals.

Introduction

Marking behaviour has long been regarded as an important component of animal social communication (THIESSEN and RICE 1976), although its function is still obscure. A number of hypotheses to explain why animals mark have been put forward ranging from deterrence of intruders (HEDIGER 1949) to establishment of a familiar smell within the territory (JOHNSON 1973), the latter attempting to explain why animals often mark as frequently inside their territories as on the borders. A more recent hypothesis proposes that scent advertises the identity of a territory inhabitant to an intruder, enabling the latter to assess the holder's status (GOSLING 1982), thus avoiding costly fights. Marking is also considered to be associated with dominance in many species (RALLS 1971; STODDART 1976; BROWN and MCDONALD 1985; KAPPELER 1980; SOMERS et al. 1990). Marking behaviour and its relation to dominance is investigated here in a group-living viverrid, the yellow mongoose, *Cynictis penicillata*.

Cynictis is a monotypic genus in the family Viverridae, limited to the southern African subregion (SMITHERS 1983). Feeding habits and reproduction have received some attention (MICHAELIS 1972; HERZIG-STRASCHIL 1977; LYNCH 1980), together with the species' implied role as a rabies vector (ZUMPT 1969, 1976) but little is known of its behaviour (EARLE 1977, 1981). *Cynictis* exhibits a degree of sociality intermediate between the highly social and solitary mongooses (WENHOLD 1990). Group sizes varying from single or paired animals to 10 or more have been reported (ROWE-ROWE 1978; ZUMPT 1976; PRINGLE 1977; DU TOIT 1980; STUART 1981; EARLE 1981; SMITHERS 1983). Animals inhabit a communal burrow system but forage alone. Colonies are territorial, male intruders being chased away while females are tolerated, especially during the mating season (WENHOLD 1990). Defenders are in most cases male residents. Territories are marked by all group members

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and this study investigates the various marking modes employed from temporal, spatial and individual aspects.

Material and methods

The study was conducted on Big Island in the Vaal Dam (26° 52″ S, 28° 11″ E), Transvaal, a temporary island of approximately 200 ha which is a peninsula for most of the year. At least 11 mongoose colonies were present on the island. The study colony consisted of 13 individuals (4 adult ♂♂, 3 adult ♀♀, 5 juvenile ♂♂, 1 juvenile ♀) and was habituated to observer presence during an initial period of 5 months. Adults were animals over 1 year old, juveniles 1 year old or less. The data on which the following analyses were based were collected on a daily basis during the 9 month period subsequent to habituation (April–December 1987) for a total of over 900 h. Mongooses were identified individually by means of natural markings and scars.

Observations were made using 10 × 50 Bencon binoculars. Since marking activities were of short duration, absolute frequency of occurrence of various marking modes were recorded using all events sampling when the animals were in groups and focal animal sampling during foraging (Altmann 1973). Observations were timed to cover the entire day from first emergence from the burrow system in the morning to return to the burrow at midday or night. Focal animals were followed for as long a period as possible until they were lost to sight. Focal observations on individuals of less than 15 min duration were not included in the analysis since they would tend to bias the results in favour of areas around the burrow systems. A different focal animal was selected each day to prevent continuity effects. Data were entered into a computer using a standard database program and further analyses were conducted using standard statistical packages. Statistical tests used are mentioned at appropriate points in the text and the level of probability given is two-tailed in all cases.

Marking frequency

Since the time periods over which individuals were observed varied, and different focal animals were observed on different days, rates of marking were calculated (mean rate/h/day/animal) to allow comparison between individuals. For statistical analyses, the daily rates of occurrence were considered independent since observations on the same animal were separated by at least seven days. Individual marking rates were calculated separately for the five different modes of marking observed.

Location of marking sites

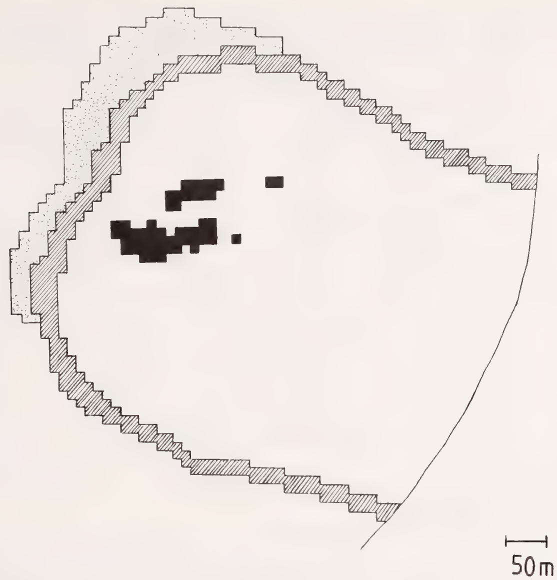
The 21,300 m^2 territory was divided into 10 × 10 m grid squares to determine marking frequency in various areas. The rate of occurrence of marking in each grid square was then calculated ie.mean marking frequency/h that the animal was observed in a particular square. Grid squares were then allocated to four categories: a. inside the territory but not in the vicinity of a burrow, b. within the territory and containing a burrow, c. on the territory border, d. outside the territory (Figure). The territory border was considered as the approximately 20 m wide fringing strip which was as far as an animal would either chase an intruder out of its territory or, conversely, how far it was chased after intruding in the neighbouring territory. The rates of occurrence of various marking behaviour patterns were determined for the four areas. The marking rates of various classes of animal in the same area were also calculated.

Results

Description of marking activities

Cynictis marks objects by four means. Anal marking, using secretions of the peanut-sized anal glands on either side of the anus, is the most common. The animal squats with the tail arched and presses the glands briefly on the substrate. Sniffing the site usually precedes marking and may follow it. In general, only a single mark is deposited on a low object, usually a stone or branch. A handstand posture typical of several other viverrids was not observed and anal dragging was rare.

Objects are also marked with a glandular area on the cheek using a wiping motion, sometimes repeated with the same or the alternate cheek. The object is stroked in a continuous movement from snout to eye. Typical objects are branches and patches of bare earth, small objects being steadied with the forepaws. The action is often preceded by



The territory of the study colony divided into 10 × 10 m^2 grid squares. The shoreline of the island is on the right. Shaded squares contain burrows, open squares are territory areas without burrows, hatched squares indicate the border of the territory and dotted squares show the areas outside the territory that were visited by group members

sniffing, and frequently followed by wiping the entire side of the body on the ground, termed side-wiping. The functional significance of the latter is not clear, since there does not appear to be any epidermal glandular tissue in this region of the body. However, side-wiping sites are often covered with dried mongoose faeces and it is possible that this behaviour is a form of "self-anointing", faecal odour being transferred by this means from one site to another. Frequently used side-wiping sites, which are usually situated next to a bush or a clump of grass, are recognisable as depressions in the ground devoid of any debris except the faeces deposited there at intervals.

Defaecation and urination can be considered as secondary ways of marking a territory. Specific defaecation sites (middens) are present, at least one being situated near every set of burrows. On emerging from the burrows in the morning, one of the first actions is to approach the midden, sniff at the faeces present, and then defaecate. This is performed from a squat with the tail arched as in anal marking, but without the anus touching the ground. Animals also defaecate at communal sites scattered throughout the territory and usually associated with secondary burrows. These are burrows used, usually by single animals, to sleep in during the heat of the day or occasionally overnight. The faeces, especially, have a strong and distinct odour, possibly from secretions of the anal gland covering them.

The same squatting posture is used by both sexes during urination, which also takes places primarily at middens, although dominant females may also urinate with one hind leg lifted. Urination also occurs at sites throughout the territory during foraging excursions.

Marking frequency

The daily rates/h of various marking modes were calculated for each animal and their means determined. The mean rates for different sex and age classes are shown in table 1.

Table 1. **Mean marking rates per hour for different sex and age classes**

Class	N	Mean marking rate/hour					
		am	sw	cw	sm	ur	def
Dominant male	1	0.54	0.02	0.20	0.75	0.0	0.39
Subordinate adult males	3	0.83	0.46	0.55	1.83	0.06	0.47
Juvenile males	5	0.41	0.32	0.31	1.04	0.14	0.61
All adult males	4	0.75	0.37	0.46	1.58	0.04	0.45
All males	9	0.56	0.34	0.37	1.27	0.10	0.54
Dominant female	1	0.11	0.07	0.10	0.28	0.0	0.68
Subordinate adult females	2	0.20	0.28	0.15	0.63	0.11	0.38
Juvenile females	1	0.0	0.0	0.0	0.0	0.0	0.56
All adult females	4	0.16	0.20	0.13	0.49	0.07	0.50
All females	5	0.15	0.18	0.12	0.44	0.06	0.50
All Adults	7	0.47	0.29	0.30	1.06	0.05	0.47
All Juveniles	6	0.38	0.29	0.29	1.00	0.13	0.61

am = anal marking, sw = side wiping, cw = cheek wiping, sm = scent marking (sum of am + sw + cw), ur = urination, def = defaecation.

Anal marking (am), cheek wiping (cw) and side-wiping (sw) rates were added to give a mean scent marking (sm) rate. The data following were tested for significant differences using the Mann-Whitney U-test.

Subordinate adult males have a significantly higher anal marking rate than the dominant male ($p < 0.05$). Males in general anal mark significantly more than females, whether only adults ($p < 0.05$) or all age groups of both sexes are compared ($p < 0.01$). Subordinate adult males also side-wiped significantly more than the dominant ($p < 0.05$) and adult males more than adult females ($p < 0.05$). All males side-wiped significantly more often than all females ($p < 0.02$). For cheek wiping, the only significant difference found was for subordinate males, which have a higher rate than the dominant ($p < 0.05$). Although not significant, all males tend to cheek wipe more than all females ($p < 0.07$).

Subordinate males also had a higher rate of scent marking in general than the dominant male ($p < 0.0005$) and subordinate females marked more than the dominant female ($p < 0.05$). Adult males had a higher marking rate than adult females ($p < 0.02$) and juvenile males a higher one than the juvenile female ($p < 0.02$). All males together thus scent mark more than all females ($p < 0.002$).

No significant differences were found between any of the age and sex classes for urination and defaecation ($p > 0.05$) but subordinate adult males had significantly higher defaecation rates than the dominant male ($p < 0.05$).

Location of marking sites

The rate of occurrence per hour of various types of marking was determined for each individual in each grid square in which it was observed. The mean data for age and sex classes in each of the four areas are shown in tables 2–5.

In grid squares containing a burrow system (Tab. 2), the only significant difference found was between adult and juvenile males, adult males having a significantly higher rate of scent marking in general than juveniles ($p < 0.001$; $p > 0.1$ in all other cases).

No significant differences were found in marking rates between any age or sex category in grid squares within the territory which did not contain a burrow system (Tab. 3), ($p > 0.1$ in all cases).

Adult males anal marked and side-wiped in the border area significantly more than

juvenile males ($p < 0.05$, Tab. 4). Their rate of all scent marking activities combined was also significantly higher than that of juveniles ($p < 0.01$). The dominant male was never observed marking on the border although he visited it. The dominant and the juvenile females were also never seen on the border of the territory throughout the study period. The data for females is therefore based only on observations from subordinate adults. Subordinate adult females anal marked the border area significantly more than juvenile

Table 2. **Mean marking rates in territory grid squares containing a burrow system**

Class	N	Mean marking rate/hour					
		am	sw	cw	sm	ur	def
Dominant male	1	0.24	0.0	0.24	0.48	0.0	0.0
Subordinate adult males	3	0.54	0.29	0.24	1.07	0.06	0.06
Juvenile males	5	0.42	0.33	0.24	0.98	0.04	0.07
Dominant female	1	0.10	0.02	0.05	0.17	0.09	0.03
Subordinate adult females	2	0.18	0.02	0.09	0.29	0.01	0.10
Juvenile females	1	0.0	0.0	0.0	0.0	0.0	0.0

am = anal marking, sw = side wiping, cw = cheek wiping, sm = scent marking (sum of am + sw + cw), ur = urination, def = defaecation.

Table 3. **Mean marking rates in territory grid squares without a burrow system**

Class	N	Mean marking rate/hour					
		am	sw	cw	sm	ur	def
Dominant male	1	2.50	0.0	0.0	2.50	0.0	0.0
Subordinate adult males	3	0.23	0.70	0.24	1.17	0.02	0.04
Juvenile males	5	0.48	1.01	0.25	1.74	0.02	0.05
Dominant female	1	0.0	0.0	0.0	0.0	0.0	0.0
Subordinate adult females	2	0.11	0.08	0.05	0.23	0.0	0.01
Juvenile females	1	0.0	0.0	0.0	0.0	0.0	0.0

am = anal marking, sw = side wiping, cw = cheek wiping, sm = scent marking (sum of am + sw + cw), ur = urination, def = defaecation.

Table 4. **Mean marking rates for grid squares on the territory border**

Class	N	Mean marking rate/hour					
		am	sw	cw	sm	ur	def
Dominant male	1	0.0	0.0	0.0	0.0	0.0	0.0
Subordinate adult males	3	4.67	4.91	2.08	11.66	0.05	0.36
Juvenile males	5	1.49	2.75	0.78	5.02	0.57	0.26
Dominant female	1	0.0	0.0	0.0	0.0	0.0	0.0
Subordinate adult females	2	2.40	0.0	1.11	3.51	0.0	0.21
Juvenile females	1	0.0	0.0	0.0	0.0	0.0	0.0

am = anal marking, sw = side wiping, cw = cheek wiping, sm = scent marking (sum of am + sw + cw), ur = urination, def = defaecation.

($p < 0.05$) but not subordinate adult males and were never observed side-wiping or urinating there.

Subordinate adult males had a significantly higher rate of scent marking in outside the territory than did juvenile males ($p < 0.001$, Tab. 5). Amongst females, only the juvenile had a significantly higher rate of defaecation outside the territory than the subordinate adults ($p < 0.001$). Females were never observed side-wiping outside the territory.

Table 5. **Mean marking rates for grid squares outside the territory**

Class	N	Mean marking rate/hour am	sw	cw	sm	ur	def
Dominant male	1	0.31	0.0	0.0	0.31	0.0	0.0
Subordinate adult males	3	4.39	3.05	1.10	8.54	0.14	0.01
Juvenile males	5	1.44	0.55	0.02	2.01	0.0	0.23
Dominant female	1	0.0	0.0	0.0	0.0	0.0	0.0
Subordinate adult females	2	0.04	0.0	0.16	0.20	0.04	0.04
Juvenile females	1	0.0	0.0	0.0	0.0	0.0	1.15

am = anal marking, sw = side wiping, cw = cheek wiping, sm = scent marking (sum of am + sw + cw), ur = urination, def = defaecation.

Comparison between areas

To determine whether different classes of animals showed significant differences in marking modes in various areas of the territory, rates were compared using the Kruskal-Wallis test (Siegel 1956). The level of significance in all cases is 0.05. Since this test compares the mean of the ranks given to the data points in the samples, the results in some cases do not appear to reflect the differences between the mean rates shown in the tables.

For grid squares containing a burrow system vs those in the remainder of the territory, the following significant differences were found: adults anal marked and cheek wiped significantly more often in the vicinity of the burrows than elsewhere in the territory, juveniles showing the opposite tendency. There were no differences between side-wiping rates, except for juvenile males which performed this behaviour significantly less often near burrows. For all classes of animals, defaecation and urination take place more often near burrows than in the remainder of the territory.

Anal marking, side-wiping and cheek wiping rates were all higher on the border than in areas of the territory away from the burrow systems for all classes of animal. Males defaecated more on the border than did females. Only juvenile males urinated more on the border than inside the territory away from the burrows. All other differences were non-significant.

A comparison of border areas with areas around burrow systems showed a significantly higher rate of anal marking at the border for subordinate males and females while the opposite was true of juvenile males and the two dominant animals. Subordinate adult males also had a higher rate of side-wiping at border vs burrow areas than females. Juvenile males showed no significant difference. The reverse was true for cheek wiping. Here, juvenile males cheek wiped more at the border than near burrows, other classes of animal showing no difference. No differences were found for defaecation in the two areas. Subordinate adult males, however, had higher urination rates near burrows.

Comparison of marking rates between grid squares on the border and those outside the territory in which group members were observed showed that subordinate adult males and females had a higher rate of anal marking on the border than outside it. Other classes of

animals, with the exception of the dominant female who did not visit the border, anal marked equally frequently in both areas. No female side-wiped outside the territory, otherwise all classes had significantly higher side-wiping and cheek wiping rates on the border than outside. Defaecation was significantly higher outside the territory for subordinate adult males while subordinate adult females and juvenile males showed no significant difference. Juvenile males, however, urinated more outside the territory than on the border.

Marking and territorial defence

The frequency with which individuals marked/10 h and were observed attacking and chasing intruders in the territory/10 h shown in table 6. There was a highly significant relationship between marking and territorial defence (Spearman's rho correlation, r_s = 0.7701, N = 12, p = 0.03). Of all ♀♀ only subordinate ♀2 was observed to attack strangers, the majority of the defence activities being performed by the adult and older juvenile males.

Table 6. **Mean rates/10 hours of attacking intruders and marking for each group member**

	Adult ♂♂			Adult ♀♀			Juv. ♂♂					Juv. ♀
	1	2	3	1	2	3	1	2	3	4	5	1
Attacks	2.1	2.4	1.1	0	1.0	0	0.4	1.0	0.7	0	0	0
Marking	7.5	25.3	18.3	2.8	2.5	6.2	4.6	16.8	15.9	1.6	1.9	0.2

Discussion

Probably the most interesting aspect of this study is that all modes of territorial marking are performed more frequently by subordinate adults than by dominant ones, in contrast to Earle's (1977) statement. This is not typical for mammals (see Ralls 1971; Eisenberg and Kleiman 1972 and Brown and MacDonald 1985 for reviews) where dominant males, especially, are the ones most involved in territorial advertisement and defence. However, in the yellow mongoose, it is the subordinate adult males which are more involved in territorial defence than the dominant male and have their highest marking rates at the territory border and in fringing areas.

The finding that males mark more in general than females has its parallels in other mammalian species (Johnson 1973; Thiessen and Rice 1976). Although a tendency for adults to mark more than juveniles has been reported in the literature (Thiessen and Rice 1976), this was not substantiated for the yellow mongoose. Adult males marked more than juvenile males, but this was not true for adult females. There was a strong correlation between marking and active territorial defence in this species, females playing little part in the latter. The study period coincided with puberty onset in the juveniles and for a related species, the dwarf mongoose *Helogale undulata*, juveniles were found to be amongst the most active group members in territorial defence (Rasa 1977) and also to have high marking rates (Rasa 1973). Thus the finding that juvenile males mark as often as adults may reflect their active role in territory protection.

The study has also shown that the areas most frequently marked by subordinate males and females are sites at the territory border and in fringing areas while the dominant female and juvenile females never visit the border, confining their marking to the territory interior around the burrows. The dominant male also marks predominantly within the territory.

Adult subordinate males anal mark and sidewipe most frequently at the border and outside the territory, subordinate adult females anal mark most frequently there. These marking modes are the ones most likely to carry identity cues, as has been found in both dwarf mongooses (Rasa 1973) and small Indian mongooses *Herpestes auropunctatus* (Gorman 1976). Juveniles urinate and cheek wipe most frequently in border areas, juvenile males extending the increased urination rate to sites fringing the territory. Cheek wiping and urination carried no identity cues in dwarf mongooses (Rasa 1973) but cheek wiping was indicative of high excitement. Juvenile marking in border areas is thus likely to have other connotations than that of the subordinate adults.

The data suggests that both Johnson's (1973) familiarity hypothesis and Gosling's (1982) assessment hypothesis may apply to the yellow mongoose. The high marking rates observed in territory areas containing a burrow system as opposed to those without one suggest that odour is preferentially deposited near major resting sites. The concentration of marks around burrows is more likely to be associated with provision of a familiar odour for inhabitants rather than with intruder deterrence, concurring with Johnson's hypothesis. Gosling's hypothesis, however, suggests that marks within a territory should be evenly distributed to increase an intruder's likelihood of encountering them and enabling it to assess the territory owner. The tendency to mark outside the territory using modalities carrying identity cues, with the highest scent marking rate occurring on the border, may establish an odour gradient external to the territory itself, indicating to an intruder the perimeter within which it can expect attack. Since yellow mongooses from different groups frequently encounter each other outside their territory borders, assessment may take place before the territory is penetrated. These marks have no deterrent effect, intruders sniffing them and then continuing on into the territory, as found for other carnivores (Leyhausen 1965; Scott 1967), Hediger's (1949) deterrence hypothesis does not appear to hold for this species.

The surprising finding that it is the subordinate adult males and subordinate females that mark more at the border than within the territory, and that the dominant animals rarely visit these areas, suggests that these marks may serve a second advertising purpose for subordinates. Subordinate males disperse from their natal group when adult, usually to neighbouring groups (Wenhold 1990), as do subordinate females. Females also cross territory borders when in oestrus and are mated by males from a neighbouring group (Wenhold 1990). The deposition of anal gland scent in areas where it is most likely to be encountered by neighbours may serve to advertise the age, sex and reproductive state of the marker, as well as familiarising members of neighbouring groups with the marks of potential immigrants and possibly facilitating the transfer of individuals between colonies.

Animals unlikely to disperse or mate or be mated outside the colony either never visited the territory border (the dominant and juvenile females), did not mark there (the dominant male), or had low rates of identity carrying marks in this area (juvenile males). Since the marking frequency of subordinate females does not appear to correlate with territorial defence activities as it does in males, another hypothesis to explain this high female marking rate on the border is suggested. By depositing the majority of their identity carrying marks in border areas, subordinate females may utilise odour cues to advertise their presence to neighbouring males for future mating purposes. For subordinate males, which are likely to have no reproductive success with females in their natal colonies (Wenhold 1990; Rasa et al. 1992), high marking rates on the border may also be a means of advertising their existence to neighbouring females, with which they have been observed to mate. Marking in this species may thus not only play a role in assessment for intruders and familiarity for territory inhabitants but may also serve a secondary purpose as a major means of sexual advertisement for subordinates, especially females, to attract prospective mates from neighbouring territories.

Acknowledgements

The authors would like to thank the Rand Afrikaans University for permission to work on their property and the Foundation for Research and Development for a grant (to A. Rasa) for partial support of the fieldwork. Special thanks are due A. van Zyl for compling the computer programmes.

Zusammenfassung

Territoriumsmarkierung bei der Fuchsmanguste Cynictis penicillata: sexuelle „Reklame" für untergeordnete Tiere?

Bei der Fuchsmanguste (*Cynictis penicillata*), einer in Kolonien lebenden Viverridenart, wird Territoriumsmarkierung von allen Gruppenmitgliedern durchgeführt. Adulte untergeordnete Tiere, sowohl Männchen als auch Weibchen, markieren häufiger als dominante und juvenile Tiere beiderlei Geschlechts. Die Duftstoffe, die Identitätsmerkmale beinhalten, werden besonders an Territoriumsgrenzen und außerhalb des Territoriums abgelegt. Adulte subordinate Gruppenmitglieder sind zudem in der Verteidigung des Territoriums am aktivsten. Innerhalb des Territoriums findet Markierung hauptsächlich um die Wohngänge herum statt, und dominante Tiere markieren entweder nicht an den Territoriumsgrenzen (dominantes Männchen) oder besuchen das Grenzgebiet nicht (dominantes Weibchen). Untergeordnete Männchen, die einen geringeren Fortpflanzungserfolg innerhalb der Gruppe aufweisen, wandern gewöhnlich in benachbarte Territorien ab. Untergeordnete Weibchen überqueren die Territoriumsgrenze, wenn sie im Oestrus sind, und werden auch von Männchen der benachbarten Gruppen begattet. Folglich markieren gerade die Tiere, die am ehesten Fortpflanzungsmöglichkeiten außerhalb der Geburtskolonie suchen, häufiger in einem Gebiet, wo der Duft von Koloniefremden angetroffen werden kann. Es wird die Hypothese aufgestellt, daß Markieren bei dieser Art außer als Vertrautheitszeichen und Besitzanspruch des Territoriuminhabers darüber hinaus als Mittel zur sexuellen „Reklame" für untergeordnete Tiere eingesetzt wird.

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Authors' addresses: Prof. Dr. O. A. E. Rasa, Abt. Ethologie, Zoologisches Institut, Universität Bonn, D-53115 Bonn, Germany, and B. Wenhold, Dept. of Veterinary Science, University of Pretoria, Onderstepoort, R. S. Africa

Z. Säugetierkunde 59 (1994) 139–152

ISSN 0044-3468

Observations éthologiques sur *Bubalus (Anoa) quarlesi* Ouwens, 1910 (Ruminantia, Bovidae) en captivité

By F. Feer

Museum National d'Histoire Naturelle de Paris, Brunoy, France

Reception du Ms. 1. 3. 1993
Acceptation du Ms. 10. 12. 1993

Abstract

Ethological observations on Bubalus (Anoa) quarlesi Ouwens, 1910 (Ruminantia, Bovidae) in captivity

Described individual and social behaviour of captive *Bubalus (Anoa) quarlesi* for comparison with known Bovinae and other Bovidae. A group of 3 males and 3 females was observed during a total of 110 hours over two periods. Many behavioural characters like horning, pawing the ground, frontal pushing of partner, frequent social licking, frontal fighting and male mating posture were common with known Bovinae, but others, typical of the group like herding, were absent. Coupling pawing the ground with urination and elements of male hierarchical and sexual display were similar to other Bovinae. The paucity of demonstrative and visual effects relates the Anoa to small forest ruminants. Except for the privileged relations between adult female and her young daughter, the social life of the Anoa appeared rudimentary as for species living in similar habitat.

Introduction

Les Bovinés (tribu des Bovini) sont phylogénétiquement divers (Bohlken 1958), se répartissent sur plusieurs continents et occupent un large éventail de milieux, depuis la forêt tropicale dense jusqu'à la savane (Walker 1983). Le genre *Anoa* ne se trouve que dans les forêts pluviales et il est endémique de Sulawesi (Iles Célèbes). Très proche du Buffle d'eau asiatique (*Bubalus bubalis*), il est actuellement considéré comme un sous-genre de *Bubalus* (Haltenorth 1963; Groves 1969) bien que certains auteurs en aient fait un genre distinct. Dolan (1965) considère qu'il n'y a qu'une espèce et 3 sous-espèces (*depressicornis, fergusoni* et *quarlesi*) mais Groves (1969), dont j'ai adopté le point de vue, distingue deux espèces: l'Anoa de plaine, *B. (Anoa) depressicornis* (H. Smith, 1827) et l'Anoa de montagne, *B. (Anoa) quarlesi* (Ouwens, 1910) qui est l'objet de cette étude. Le manque de specimens dans les collections et de données provenant de la nature fait que la discussion sur leur taxonomie reste encore ouverte. *B. (Anoa) quarlesi* est le plus petit Boviné actuel, (hauteur au garrot environ 70 cm). Dolan (1965), Groves (1969) et Frädrich (1973) décrivent les 2 espèces et les variations morphologiques possibles. Les animaux que j'ai observé présentent des taches claires sur les joues et sous le menton nettement moins étendues que celles de *B. (Anoa) depressicornis.*

Il n'existe que quelques données parcellaires sur le comportement et la reproduction des 2 espèces (Dolan 1965; Pournelle 1965; Frädrich 1973). Des études comportementales sont en cours en Allemagne, mais les observations dans la nature manquent totalement. Ce travail ne présente pas un éthogramme de l'Anoa de montagne mais il décrit les principaux comportements pour situer cette espèce au sein des Bovinés et par rapport aux Bovidés.

Matériel et méthodes

Les observations ont été faites au Zoo de Krefeld (Allemagne) durant les mois de mai 1989 et septembre 1990. Durant la première période les animaux (Tab. 1) occupaient un enclos de 150 m^2 avec

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Tableau 1. **Caractéristiques des Anoa de montagne observés au zoo de Krefeld**

Sexe	Date et lieu de naissance	Dénomination	Observations
Mâle	20. 1. 1975 Berlin	Mâle adulte	Pelage noir
Mâle	8. 10. 1987 Krefeld	Jeune mâle	Fils de la femelle adulte, brun
Femelle	31. 5. 1977 Berlin	Femelle adulte	Pelage brun allaitante en 1990
Femelle	13. 9. 1986 Krefeld	Jeune femelle	Fille de la femelle adulte, brune

des gradins de pierre et des arbres et, durant la deuxième, un enclos de 600 m^2, planté d'arbustes et décoré de rochers. Les observations totalisent 86 heures en mai 1989 et 24 heures en septembre 1990 durant les périodes d'activité maximum des animaux, c'est à dire le matin dès leur sortie des boxes où ils passaient la nuit et en fin d'après-midi. Les comptages des interactions sociales pacifiques et agonistiques ont été faits sur les 4 animaux simultanément, puisqu'ils étaient aisément identifiables et pouvaient s'observer ensemble pendant plus de 95 % du temps. Les descriptions des comportements ont été complétées de mesures chronométrées et de photographies. La comparaison des fréquences a été faite par le test G avec la correction de William.

Résultats

Comportement individuel

Miction et défécation: les postures de miction diffèrent selon les sexes mais celles de défécation sont semblables. Les mâles urinent en reculant légèrement les membres postérieurs (Fig. 1A). Les femelles abaissent la croupe en fléchissant les membres postérieurs et lèvent la queue pendant la miction (Fig. 1B). Contrairement à ce qui se passe chez la plupart des Ruminants, la croupe est plus abaissée lors de la défécation qu'elle ne l'est au cours de la miction des femelles. Les membres postérieurs sont plus fléchis et leurs extrémités sont écartées (Fig. 1C). Il n'a pas été observé de variation notable selon les individus.

Lever de tête et du cou: la tête est levée et tournée dans le même temps sur son axe. Le mouvement varie en intensité depuis le relèvement de la ligne du menton à environ 45° accompagné d'une faible inclinaison de la tête jusqu'au lever à la verticale avec une rotation d'un quart de tour de la tête se présentant de profil vers l'avant, les cornes en contact avec le cou (Fig. 2). Les jeunes individus font ce mouvement en tournant sur eux-mêmes ou en avançant la tête renversée en arrière. Il semble que le mouvement initial du menton soit dirigé vers l'origine de la stimulation qui l'a provoqué (congénère, personne proche, bruit ou odeur insolite) mais cela reste difficile à contrôler pour les jeunes. Tandis que le lever de tête est fréquent chez les autres animaux, il est très rare chez le mâle adulte; il est seulement ébauché et débouche rapidement sur la posture de parade hiérarchique. Frädrich (1973) évoque brièvement un comportement analogue au lever de tête dans un contexte de menace.

Frottement de la tête: le front, la base des cornes, les côtés de la tête, les joues et plus rarement le bord du museau sont frottés avec des mouvements de va et vient sur divers supports fixes. Durant la deuxième période d'observation, les animaux passaient la tête, le front ou la joue, en un seul mouvement, dans les branches de petits arbustes et le mâle adulte frottait son front sur le sol gazonné (Fig. 3A), stade intermédiaire entre le travail du sol avec les cornes et le passage des cornes dans un arbuste.

Râclement des cornes: le râclement des cornes sur un support rigide résulte le plus souvent d'une amplification des mouvements de frottement avec la tête. Les traces les plus

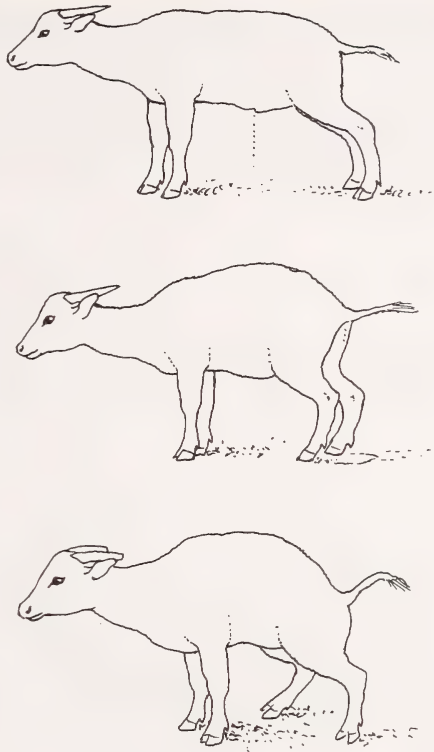

Fig. 1. a: Miction du mâle; b: miction de la femelle; c: défécation du mâle (dessins d'après photographies)

visibles des frottements de tête et du râclage des cornes apparaissaient sur l'arbre situé au centre du premier enclos, dont l'écorce était arrachée sur une grande surface jusqu'au niveau du sol. Durant la deuxième période, le mâle adulte, qui faisait à lui seul 48 % de ces comportements (n = 29), répétait le mouvement avec force, en alternance avec un grattage du sol avec la patte avant dans plus de la moitié des cas. Une amplification du mouvement conduisait parfois au frottement du front puis au creusement du sol avec les cornes devant l'arbuste. Le travail du sol avec les cornes, effectué parfois en appui sur un métacarpe, a été observé à 2 reprises chez la femelle adulte. L'action de passer des branches coupées entre les cornes et de secouer la tête ou de les transporter sur quelques mètres (Fig. 3B) s'apparente à un jeu, le plus souvent observé chez les jeunes animaux (87 %, n = 63, G = 10,55, P < 0.01). Le jeune présent à la deuxième période soulevait avec les cornes les mottes de gazon arrachées par sa mère.

Grattage du sol: après un contrôle olfactif de la place, le sol est gratté avec une patte antérieure, plus rarement avec les 2 successivement. Le mouvement de la patte est peu accentué et la tête est basse, le museau proche du sol (Fig. 3C). Le mâle adulte est le seul animal à effectuer le grattage du sol dont il accompagne 54 % (n = 165) de ses mictions: il avance de deux pas et urine sur la place grattée. La grande majorité des grattages est liée aux mictions (77 %, n = 117, G = 37,79, P < 0,001). Les autres ont lieu soit seuls (14 %), soit avant un râclage des cornes

Fig. 2. Etapes du lever de la tête par la femelle adulte (de gauche à droite)

dans un arbuste (7 %) et plus rarement accompagnés du frottement du front ou de la défécation. Le grattage du sol n'a jamais lieu à proximité immédiate d'un individu particulier ou en relation avec un comportement social. Il a été constaté cependant qu'il se produisait très souvent après une interaction agressive intense avec un membre du groupe ou des manifestations du même ordre dirigées vers l'extérieur. Il semble donc qu'il soit lié à une démonstration hiérarchique ou agonistique adressée à l'ensemble du groupe et/ou aux personnes connues de l'extérieur.

Comportement social

Interactions non agressives

Flairages: les contrôles olfactifs les plus fréquents ont lieu dans la région ano-génitale et sur la tête. Le plus jeune mâle flaire régulièrement les femelles à la naissance des membres antérieurs, sur le ventre et autour des cuisses. Les fréquences des flairages diffèrent entre les individus (G = 11,52, P < 0,01, n = 153) avec une plus grande activité du jeune mâle (Tab. 2). Il les dirige à 87 % sur les 2 adultes. Le flairage du pénis du mâle adulte par le jeune mâle et par la femelle adulte a été régulièrement observé.

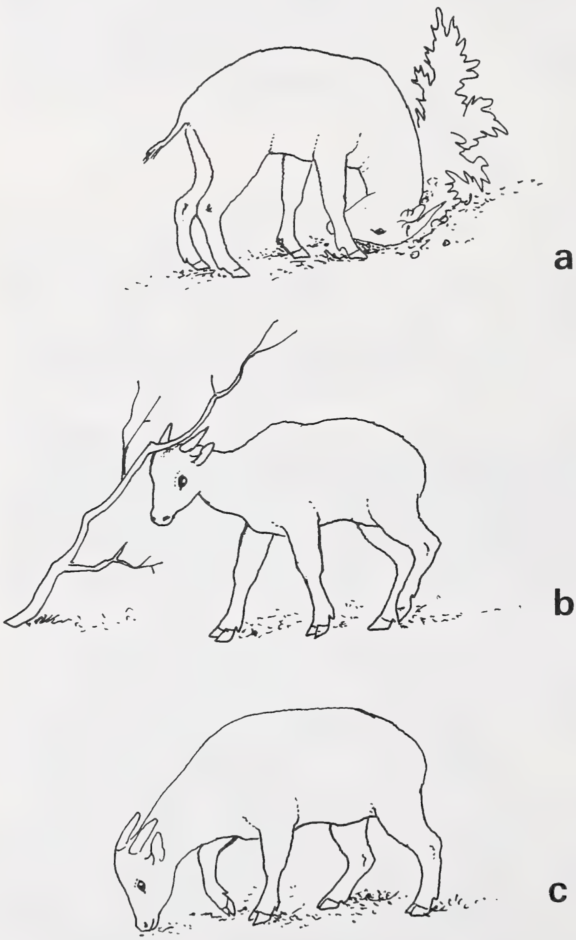

Fig. 3. a: Frottement du front sur le sol; b: jeu avec les branchages; c: grattage du sol par le mâle adulte

Contrôle urinaire: en dehors du contexte strictement sexuel du mâle contrôlant l'urine d'une femelle, le léchage de l'urine pendant la miction ou sur le sol a été observé chez tous les autres individus du groupe. Les 2 adultes lèchent occasionnellement leur propre urine.

Contact frontal: le front est posé sur le flanc, l'épaule ou le cou du partenaire; dans 60 % des cas (n = 41), il y a une brève poussée (Fig. 4A). Ce comportement peut précéder une interaction pacifique et ne déclenche en général aucune réaction défensive. Durant la première période, il est surtout observé chez la femelle adulte (59 %, n = 46, G = 146,34, P < 0,001) principalement sur le mâle adulte (G = 22,00, P < 0,01, n = 27).

Frottement de la tête: la joue, plus rarement le côté du front, le cou ou le menton

Tableau 2. **Nombre de flairages (a), de contact frontaux (b), et de frottement de la tête (c) observés dans le groupe d'Anoa durant la première période**

Animal initiateur		Animal receveur ♂ adulte	♀ adulte	♂ jeune	♀ jeune	Total
	a		10	20	4	34
♂ adulte	b		1	3	1	5
	c		3	1	0	4
	a	7		4	10	21
♀ adulte	b	25		1	1	27
	c	0		4	11	15
	a	35	20		8	63
♂ jeune	b	7	6		0	13
	c	0	16		5	21
	a	8	21	6		35
♀ jeune	b	0	0	1		1
	c	0	93	3		96

sont frottés de bas en haut, rarement de manière répétée, sur le haut des cuisses et la région anale du partenaire (Fig. 4B). Durant la première période, la majorité des observations a été faite chez la jeune femelle (70 %, n = 136, G = 68,06, P < 0,001), à 97 % sur sa mère.

Léchage social: le léchage est la forme de contact pacifique la plus prolongée entre individus. Nous ne considérerons dans ce chapitre que les léchages non sexuels, le plus souvent pratiqués sur la tête, le cou et une zone qui va du garrot à la croupe. L'animal qui veut lécher approche le partenaire par le côté ou par devant, la tête basse et le museau tendu en avant. L'invitation au léchage consiste en une immobilisation de la tête légèrement

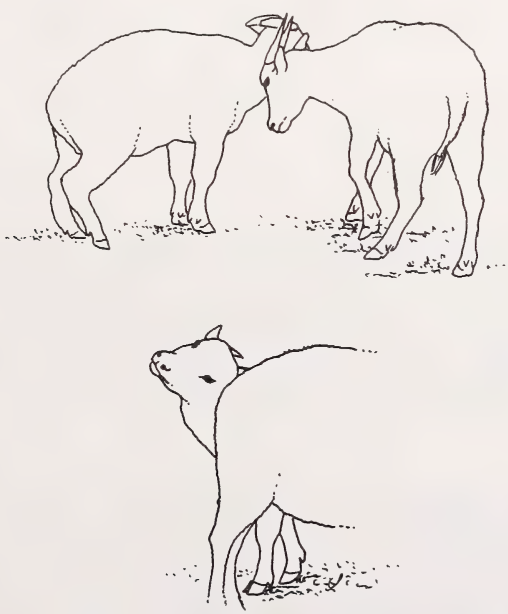

Fig. 4. a: Poussée du front par la femelle adulte sur le mâle adulte; b: frottement de la joue par la jeune femelle sur sa mère

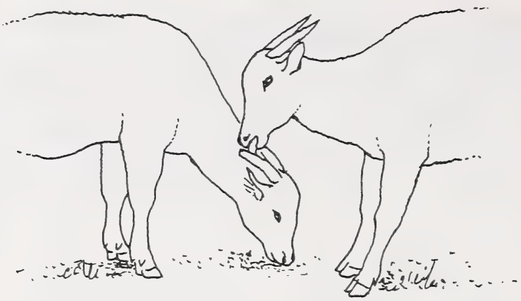

Fig. 5. Posture d'invitation au léchage par l'animal de gauche

abaissée, museau dirigé vers le sol, à proximité de la tête du partenaire (Fig. 5) puis la tête est parfois légèrement tournée, de façon à présenter la joue, ou relevée pour montrer le cou. Face à un individu qui menace, l'attitude d'invitation au léchage a un effet inhibiteur immédiat. Le léchage est le plus souvent unilatéral; quand 2 animaux se léchent, c'est toujours en alternance et jamais simultanément. De longues séances de léchage sont observées, mettant parfois en jeu 3 animaux. Les fréquences des léchages sont différentes entre les individus (G = 14,74, P < 0,01, n = 284) avec une plus grande activité du jeune mâle (Tab. 3). Les léchages entre mâles et entre femelles sont plus fréquents que les léchages intersexuels (respectivement G = 6,42, P < 0,02, n = 156 et G = 11,05, P < 0,001, n = 128). Les léchages du mâle adulte par le jeune mâle sont plus nombreux que l'inverse (G = 6,02, P < 0,02, n = 78).

Pose du menton: le menton est posé sur la partie postérieure du corps du partenaire ou plus rarement sur le garrot. Ce comportement qui fait partie du comportement sexuel normal du mâle adulte (cf plus loin) a été observé chez les jeunes, le plus souvent le mâle (G = 5,55, P < 0,002, n = 46).

Tableau 3. **Nombre de léchages entre les individus du groupe d'Anoa durant la première période**

Animal initiateur	Animal receveur				
	♂ adulte	♀ adulte	♂ jeune	♀ jeune	Total
♂ adulte		24	20	3	47
♀ adulte	14		19	39	72
♂ jeune	34	30		25	109
♀ jeune	1	30	25		56

Association au repos: les fréquences des repos solitaires par rapport aux repos en association avec un autre animal du groupe sont différentes (G = 40,27, P < 0,001, n = 205). Le mâle adulte est plus souvent seul (71 %, n = 28) que la femelle adulte (G = 26,99, P < 0,001, n = 93), le jeune mâle (G = 39,39, P < 0,001, n = 97) ou la jeune femelle (G = 29,94, P < 0,001, n = 71). Ces 3 derniers montrent un certain allomimétisme et prennent leur repos ensemble dans 15 % des cas de repos commun (n = 81). Le mâle adulte suit un rythme relativement différent et occupe préférentiellement quelques emplacements qui lui sont exclusifs.

Interactions agressives

Menace tête basse: la tête est abaissée en direction du partenaire, la ligne du front proche de la verticale et le museau près du sol. Quand le partenaire adopte une posture identique, les animaux se font face, front bas et perpendiculaire au sol (Fig. 6A). Ce comportement, également observé par Frädrich (1973), est peu fréquent (18 % des menaces, n = 70) et se produit le plus souvent entre les adultes chez qu'il semble correspondre à une lutte avortée.

Menace des cornes: la tête, en position basse, est fléchie de manière à diriger les pointes des cornes vers l'adversaire (Fig. 6B). C'est une menace plus sérieuse que la précédente.

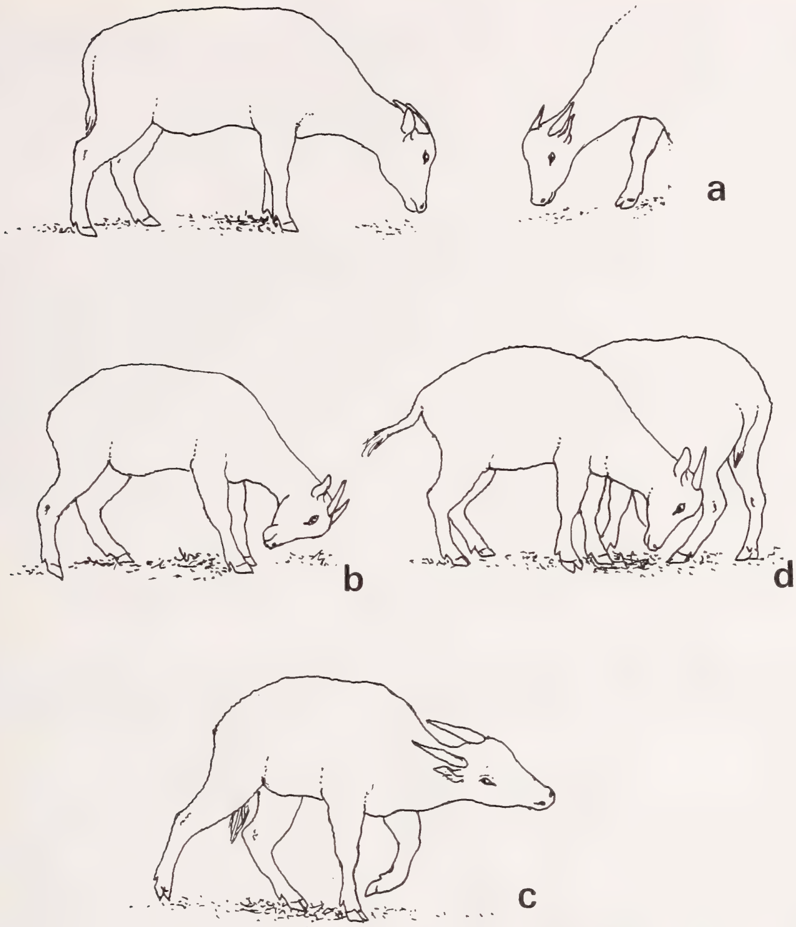

Fig. 6. a: Menace tête basse réciproque; b: présentation des cornes; c: parade hiérarchique; d: coup de cornes

Parade: le cou est porté horizontalement et le museau est tendu en avant, la tête étant tournée d'environ 45° sur son axe. Cette position est maintenue pendant l'approche du partenaire en marche rapide ou au trot (Fig. 6C) parfois jusqu'à ce que les 2 animaux soient en parallèle. La tête est le plus souvent tournée de façon à montrer les cornes au partenaire. Le mâle adulte ne parade pas en direction des autres animaux du groupe, mais toujours en réaction à une perturbation venant de l'extérieur. Ce comportement a également été observé, mais très rarement, chez la femelle adulte et le mâle vivant isolé. Frädrich (1973) publie une photographie d'un mâle en attitude de parade, les cornes dirigées vers un animal d'une autre espèce siuté dans l'enclos voisin.

Lever hiérarchique: il se compose de poussée du front ou de coup de cornes sur le flanc ou la croupe, d'appui du menton ou de la joue sur la croupe ou le garrot, d'appui d'une patte antérieure (rarement les deux) sur le corps. En réponse aux coups de cornes, l'animal couché peut allonger le cou et le menton sur le sol.

Charge agressive: l'agresseur galope droit sur son adversaire, la tête en position normale à hauteur du garrot ou redressée avec occasionnellement les oreilles rabattues en arrière. De brefs meuglements peuvent être entendus. La charge se termine par un coup violent si le

partenaire ne fuit pas. Le mâle adulte, très agressif envers l'observateur et certains soigneurs, faisait fréquemment des charges dans leur direction, puis les redirigeait vers les animaux du groupe situés près de lui. Dans des moments d'excitation avant ou après la charge, il marchait en bloquant brièvement en l'air une patte antérieure ou postérieure, une attitude également observée chez les autres individus quand ils étaient inquiets ou excités.

Coup de front: à la différence du simple contact et de la poussée, le coup de front sur l'épaule ou le flanc est porté avec élan. Il est peu brutal à courte distance, mais peut-être violent quand il suit la charge.

Coup de cornes: après flexion de la tête, le coup de la pointe des cornes est donné de bas en haut, le plus souvent au flanc ou au ventre de l'adversaire (Fig. 6D). Des mouvements de tête répétés de bas en haut à vide ont été observés chez le mâle et la femelle adulte.

Les comportements agonistiques sans contact corporel (menace, charge) (Tab. 4) s'observent pour l'essentiel entre les 2 adultes (95 %, n = 150, G = 83,45, P < 0,001, n = 300). Le mâle adulte ne les dirige vers aucun partenaire en particulier (G = 0,02, N S, n = 142) tandis que la femelle adulte les concentre sur le mâle adulte (G = 55,83, n = 142). La fréquence des comportements agressifs directs est la plus élevée chez le jeune mâle (G = 70,53, P < 0,001, n = 444) qui montre d'ailleurs peu d'autres comportements agonistiques. Le jeune mâle les dirige principalement vers la femelle adulte qui y répond relativement peu, ce qui fait supposer qu'il existe une part de jeu dans ces échanges. Au contraire, les relations interadultes sont tendues, caractérisées pour la femelle et pour le mâle par une faible fréquence relative de comportements directs par rapport aux comportements indirects (respectivement G = 5,35, P < 0,05, n = 196 et G = 6,53, P < 0,02, n = 56).

Tableau 4. **Nombre de comportements agonistiques indirects (menaces, charges: a) et directs (coup de front, de cornes, lever: b) dans le groupe d'Anoa observé durant la première période**

Animal initiateur		Animal receveur				
		♂ adulte	♀ adulte	♂ jeune	♀ jeune	Total
♂ adulte	a		23	31	17	71
	b		5	22	13	40
♀ adulte	a	65		5	1	71
	b	33		7	1	41
♂ jeune	a	5	3		0	8
	b	30	76		25	131
♀ jeune	a	0	0	0		0
	b	3	1	6		10

Hiérarchie: durant la première période la femelle adulte marque sa dominance par davantage de comportements indirects ou directs que le mâle adulte (respectivement G = 10,63, P < 0,01, n = 1976 et G = P < 0,001) qui cède le passage quand elle approche. Pendant la deuxième période la femelle adulte ne manifeste aucune agressivité envers le mâle adulte tandis que celui-ci montre une fréquence de comportement agonistique semblable à celle de la première période (respectivement 0,46/h et 0,33/h). Je n'ai observé aucun combat sérieux entre adultes mais d'après les soigneurs ils ont périodiquement lieu et sont très intenses. Le mâle adulte manifeste davantage son agressivité vis à vis de l'extérieur et particulièrement envers un autre mâle subadulte dans un enclos voisin durant la deuxième période. Ceci correspond bien aux observations de Dolan (1965) sur l'Anoa de plaine. Alors que les agressions entre femelles sont rares durant la première période, elles deviennent plus fréquentes pendant la deuxième, particulièrement de la part de la femelle

adulte qui allaite encore son nouveau jeune (14 observations contre 2 chez la jeune femelle qui connait son premier oestrus).

Soumission: l'animal dominé se couche, cou et menton sur le sol. Cette attitude observée chez le jeune mâle permet également d'éviter les coups de cornes portés sous le corps par la femelle adulte.

Jeu

Le jeu solitaire se manifeste par des courses au galop à travers l'enclos ou des charges vers des objets ou des oiseaux. Un animal provoque un autre au jeu en galopant dans sa direction avec des bonds désordonnés (Fig. 7A) ou avec des hochements de tête avec présentation des cornes. FRÄDRICH (1973) décrit les mêmes comportements ludiques parfois très prolongés chez les plus jeunes. Le jeu de combat consiste en poussées, front contre front ou cornes engagées, avec les têtes complément fléchies et les museaux rabattus vers l'arrière. Les corps sont face à face (Fig. 7B) ou en position parallèle, les têtes tournées l'une contre l'autre (Fig. 7C). Pour résister aux poussées de son adversaire ou à ses coups de cornes donnés sous le corps, l'un des partenaires se tient occasionnellement sur les métacarpes (Fig. 7D). Pendant l'affrontement, les animaux cherchent à se dégager pour donner des coups de front ou de cornes dans le flanc de l'adversaire. Comme ils cherchent

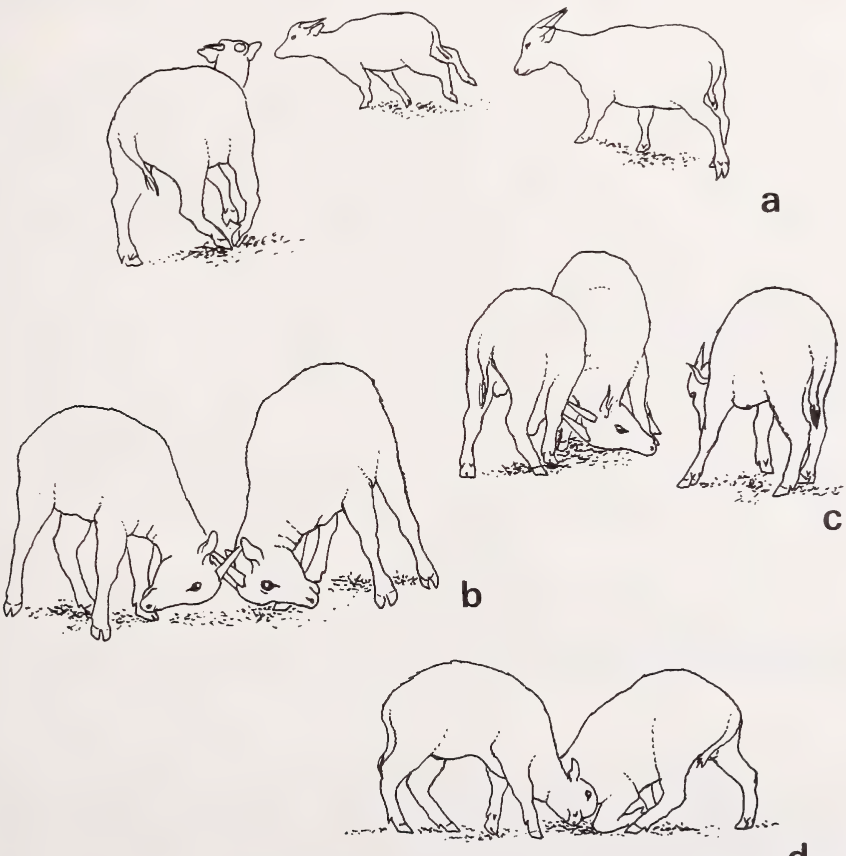

Fig. 7. Jeu social: a: galop d'invitation au jeu et poursuite à 3 animaux; b: combat de jeu, face à face; c: combat de jeu en position latérale; d: appui sur les metacarpes

également à dérober leur propres flancs aux coups, il en résulte un mouvement circulaire des deux participants parfois en position parallèle inversée. Le jeu de combat est entrecoupé de brefs arrêts face à face, têtes basses, et de poursuites au cours desquelles l'individu poursuivi rue de manière désordonnée vers son rival. Des meuglements se font entendre dans ces moments d'excitation intense. D'après les soigneurs, le combat de jeu serait tout à fait similaire au combat sérieux.

Durant la première période d'observation, la majorité des jeux avaient lieu entre les 2 jeunes (82 %, $n = 79$, $G = 47{,}02$, $P < 0{,}001$, $n = 158$). Le jeune mâle en était le plus souvent l'initiateur (73 % des invitations observées, $n = 46$, $G = 6{,}36$, $P < 0{,}02$, $n = 112$). Il invitait principalement la jeune femelle (66 %, $n = 41$) mais aussi le mâle adulte que ne répondait que rarement, tandis que la femelle adulte, pourtant moins sollicitée, jouait plus souvent avec lui (15 %, $n = 79$). Durant la deuxième période d'observation, la grande majorité des jeux se déroulaient entre la jeune femelle et le nouveau jeune de la femelle adulte.

Comportement sexuel

Contrôle urinaire: les mâles contrôlent l'état génital des femelles en léchant la vulve et ils provoquent le plus souvent la miction (Fig. 8A). Ils laissent couler l'urine sur le museau et la goûtent en sortant la langue. Le Flehmen suit fréquemment ce comportement qui peut ensuite être immédiatement renouvelé ou suivi du léchage des talons et des cuisses mouillées d'urine.

Flehmen: au cours du Flehmen la lèvre supérieure est retroussée, la bouche entrouverte et la tête un peu relevée, le front proche de l'horizontale; la tête est parfois un peu tournée de côté (Fig. 8B). Chez le mâle adulte qui fait la grande majorité des Flehmen durant la première période (91 %, $n = 129$), ce comportement est presque toujours unique et dure peu longtemps (7,9 s +/− 1,8; $n = 19$). Le Flehmen des mâles a lieu essentiellement à l'urine des femelles mais quelques observations ont été faites du mâle adulte et du mâle isolé réagissant à leur propre urine après s'être léché le pénis. La femelle adulte a effectué un Flehmen après avoir provoqué la miction de la jeune femelle, et 3 autres en réaction à diverses stimulations olfactives provenant de l'extérieur.

Parade sexuelle: le mâle suit la femelle, le cou étiré horizontalement à hauteur du garrot, le museau tendu en avant dans le prolongement (Fig. 8C). Cette posture est analogue à celle de la parade hiérarchique mais la rotation de la tête ne l'accompagne que rarement. Quand le mâle est proche de la femelle, il donne des coups de langue à vide et cherche à lui lécher la vulve pour provoquer la miction. Quand le mâle approche pour tester la réceptivité de la femelle, il avance brusquement derrière elle avec un trépignement des pattes antérieures, en relevant le cou et le menton à environ 45°, le dessous du cou venant en contact avec la croupe de la femelle (Fig. 8D). Quand les animaux sont très excités, ils font entendre de brefs meuglements.

Monte sexuelle: après la parade sexuelle et/ou le léchage vulvaire, le mâle pose son menton sur la croupe de la femelle ou monte directement (Fig. 8E). Pendant la monte le cou et le menton sont appuyés sur le dos et le garrot de la femelle (Fig. 8F); les pattes antérieures raidies enserrent ses flancs.

Discussion

Le comportement d'Anoa présente de nombreux traits communs avec différents Bovinés connus, ce qui est en accord avec son appartenance à ce taxon, basée sur les critères morphologiques. La miction et la défécation s'accomplissent séparément et sans postures particulièrement accusées, comme chez la plupart des Bovidés. Le grattage du sol comme comportement d'expression est très répandu dans tous les groupes de Bovidés à l'exception

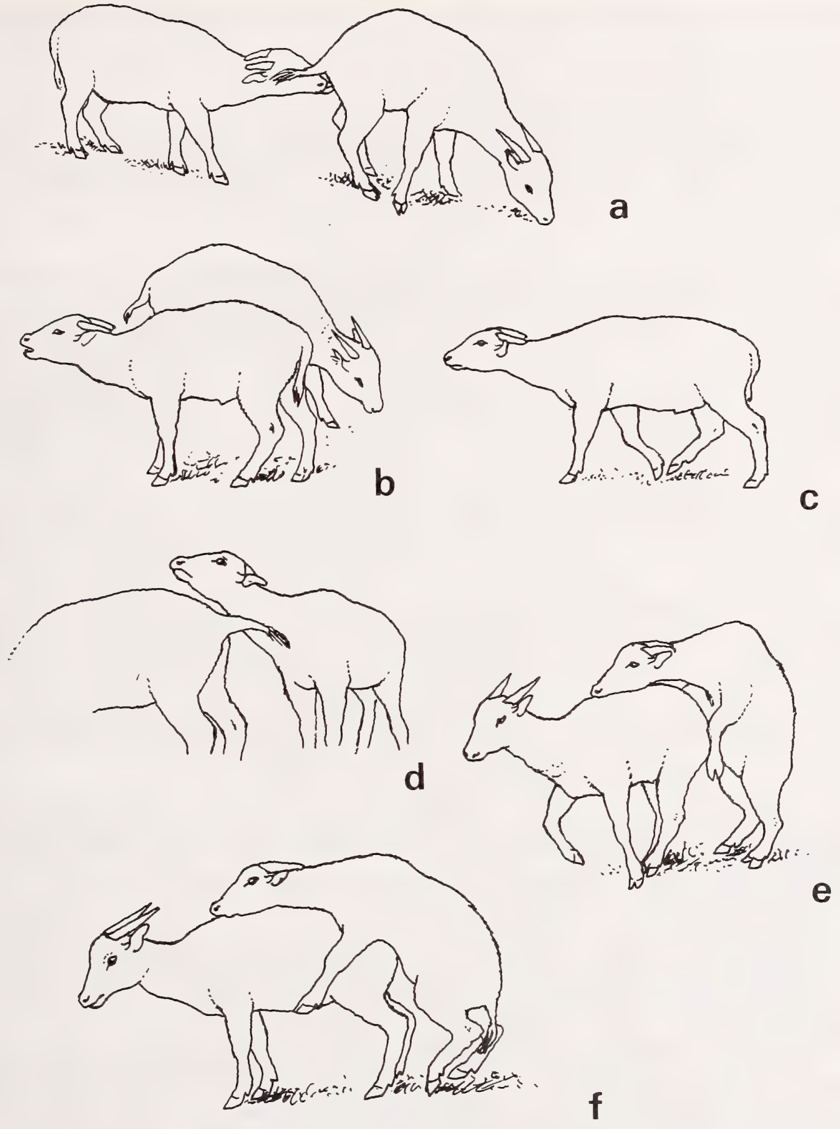

Fig. 8. Comportement sexuel: a: léchage vulvaire par le mâle provoquant la miction de la femelle; b: Flehmen du mâle; c: parade sexuelle du mâle; d: comportement précopulatoire avec trépignement des pattes antérieures; e: pose du menton et tentative de monte; f: monte sexuelle

des Tragelaphinés et de *Boselaphus*. Chez Anoa cependant il est restreint à quelques comportements particuliers du mâle alors qu'il est beaucoup plus généralisé chez la plupart des Bovinés (Schloeth 1958). Remarquons que les mouvements de grattage du sol du mâle Anoa sont beaucoup moins accusés que ceux de *Bos taurus* (Schloeth 1958). Le grattage avec les cornes, le frottement de la tête sont des comportements de confort qui ont également une fonction d'expression dynamique et sont très répandus chez les autres Bovidés (Walther 1968). Les contacts frontaux entre adultes peuvent être considérés

comme des attitudes agressives ritualisées servant au contact social mais il ne semble pas exister de comportement semblable au «Hornen» décrit par SCHLOETH (1961) chez *B. taurus. Bos javanicus* fait un frottement de joue (HALDER 1976) semblable à celui de la jeune femelle Anoa. La fréquence des léchages sociaux entre adultes rapproche davantage l'Anoa de son groupe et des Tragelaphinés (SCHLOETH 1961; WALTHER 1964) que d'autres Bovidés (WALTHER 1979). La valeur apaisante de l'invitation au léchage est connue chez *B. taurus* (SAMBRAUS 1969). L'initiateur du léchage a souvent un rang inférieur à son partenaire comme chez *B. taurus* (SCHLOETH 1961; BOUISSOU 1974) et *B. gaurus* (SCHALLER 1967).

L'imposition latérale en parallèle ou antiparallèle, très courante chez les Bovinés, n'a pas été observée chez Anoa mais il est possible qu'elle existe entre 2 mâles adultes. Les menaces et le combat frontal ne le distinguent pas de nombreux Bovidés. La position en appui sur les métacarpes sert à éviter le soulèvement par l'adversaire mais elle n'est pas une attitude typique comme chez *Boselaphus, Tetracerus* et *Alcelaphus.* La pose du menton sur la croupe de la femelle avant la monte est présente chez les autres Bovinés (SAMBRAUS 1971; LOTT 1974; HALDER 1976) mais sans mouvement latéral. La posture de monte est conforme à celle de la plupart des Bovinés, *Boselaphus, Tragelaphus.*

Certains comportements typiques des Bovinés connus sont absents chez Anoa, tandis que d'autres le rapprochent de groupes voisins. Le couplage préferentiel du grattage du sol avec la miction chez le mâle rappelle le comportement des petites espèces territoriales d'Alcélaphinés et d'Antilopinés mais il est difficile de l'interpréter en captivité. Le frottement et grattage de supports laissent des traces visibles qui pourraient avoir une valeur de marquage optique. Il est probable que chez une espèce forestière à tendance probablement solitaire comme l'Anoa, ils aient la même fonction que chez les Ruminants forestiers (DUBOST 1983; FEER 1984). Le lever de tête et du cou semble être absent chez les autres Bovinés, alors qu'un comportement assez similaire a été observée chez *Capra ibex* et *Hemitragus jemlahicus*, et chez les jeunes *Taurotragus euryceros* (HAMANN 1979). Il existe aussi chez les femelles de Tragélaphinés (WALTHER 1958).

La parade hiérarchique d'Anoa n'a pas été clairement observée chez les Bovinés. La rotation de la tête en particulier, ressemble au comportement de *Ovis canadensis* (GEIST 1966). Au cours de la poursuite sexuelle Anoa fait des coups de langue à vide comme les Caprinés, *Aepyceros* et *Boselaphus* et sa posture de parade est rare chez les Bovinés. Le «Hüten» qui caractérise de nombreux Bovinés (WALTHER 1979) est absent. Le relèvement du cou contre la femelle à la fin de la parade sexuelle, couplé à un trépignement des pattes antérieures n'a été observé que chez *B. javanicus* (HALDER 1976) et rappelle le Laufschlag rudimentaire et ritualisé de *Gazella granti* (WALTHER 1965) et *Antilope cervicapra* (DUBOST et FEER 1981).

Une partie du comportement d'Anoa a pu être modelé par son mode de vie, comme par exemple le bloquage d'une patte en l'air qui caractérise les espèces de milieux denses (WALTHER 1979). De même, la pauvreté des éléments démonstratifs visuels et la forme de la parade hiérarchique et sexuelle rapproche Anoa des petits Ruminants forestiers comme *Muntiacus, Cephalophus, Neotragus* (DUBOST 1983). Ces derniers se montrant dans l'ensemble moins grégaires que ceux des milieux ouverts (ESTES 1974; WALTHER 1979; DUBOST 1983) on peut s'attendre à trouver chez Anoa les indices d'une vie sociale relativement rudimentaire. Malgré l'exiguité des conditions de captivité qui risquent de biaiser les observations, il apparait des possibilités de vie en groupe entre femelles et subadultes (allomimétisme, fréquents léchages, jeux sociaux, association au repos). Le mâle adulte serait plus solitaire et intolérant envers un autre adulte. La femelle adulte garde des relations privilégiées avec sa fille tant qu'elle n'est pas en oestrus ou qu'elle n'a pas elle même un autre jeune. La vie sociale d'Anoa serait proche de celle des petites espèces forestières comme *Muntiacus* et *Cephalophus* (DUBOST 1980, 1983a, 1983b). Des données sur les Bovinés plus ou moins liés à la forêt comme *Bos banteng, Bos sauveli* et

paticulièrement *B. mindorensis* (Talbot et Talbot 1966) manquent pour discuter de cette question.

Remerciements

Je remercie le Dr. W. Encke, Directeur du Zoo de Krefeld et le Dr. P. Vogt pour leur accueil et leur aide sur place. Ce travail a été financé par le laboratoire d'Ecologie Générale du Muséum National d'Histoire Naturelle de Paris. Je remercie G. Dubost, A. Heymer et un critique anonyme pour leur commentaires sur le manuscript.

Zusammenfassung

Ethologische Beobachtungen an Bubalus (Anoa) quarlesi Ouwens, 1910 (Ruminantia, Bovidae) im Zoo

Zwischen Mai und September 1990 wurde im Zoo Krefeld eine Gruppe von Berg-Anoas (3 Männchen, 3 Weibchen) während insgesamt 110 Stunden ethologisch beobachtet. Individual- und Sozialverhalten werden beschrieben und die Ergebnisse, soweit möglich, mit anderen Bovinae und der Gesamtheit der Bovidae verglichen. Das Vorderlaufscharren ist ein meist mit der Miktion assoziiertes Verhaltenselement und wird nur vom erwachsenen Bullen ausgeführt. Es begleitet aber auch das Bodenhornen, Stirnreiben und Aufsteilen. Die häufigsten sozialen Kontaktformen sind das gegenseitige Kopfstoßen, das Kopfreiben auf der Kruppe des Partners und das soziale Lecken. Drohen mit gestrecktem Kopf oder mit den Hörnern sowie effektive Angriffe charakterisieren die ständig gespannten Beziehungen zwischen den Erwachsenen, während die Jungtiere häufiger den frontalen Kopfstoß anwenden oder mit dem Gehörn direkt angreifen. Drohverhalten mit gestrecktem Hals und seitlich verdrehtem Kopf ist das häufigste Element der Bullen. Soziales Spielverhalten zwischen den Jungtieren besteht aus Verfolgungen und langen Stößen Kopf gegen Kopf oder in einer sich um die Achse drehenden Antiparallelstellung. Bei einer brünftigen Kuh zeigt der Bulle dann ein Werbeverhalten, das der Rangdemonstration sehr ähnlich ist. Der hochgestreckte Kopf geht dem Aufspringen voraus und wird von Tretelbewegungen mit den Vorderläufen begleitet. Das Verhalten der Berg-Anoas zeigt zahlreiche Gemeinsamkeiten mit den übrigen Bovinae, jedoch sind deren Ausdrucksweisen weniger markant und weniger differenziert. Die Anoas besitzen unter anderem einige besondere Verhaltensweisen wie das Treten mit den Vorderläufen als ritualisierten Laufschlag und das Kopfdrehen beim Drohen, die sie mit anderen Bovidae verbinden. Sie haben auch Gemeinsamkeiten mit einigen kleinen Waldarten wie *Muntiacus* und *Cephalophus*, so etwa in ihrem Sozialverhalten.

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Adresse de l'auteur: Dr. François Feer, Laboratoire d'Ecologie Générale, MNHN, CNRS, 4, Avenue du petit Château, F-91800 Brunoy, France

Z. Säugetierkunde 59 (1994) 153–160

ISSN 0044-3468

Chromosomal reduction in an Okapi pedigree (*Okapia johnstoni*)

By P. Petit, H. De Bois, and W. De Meurichy

Division of Human Genetics, Department of Human Biology, University Hospital, Leuven and Royal Zoological Society of Antwerp, Belgium

Receipt of Ms. 1. 2. 1993
Acceptance of Ms. 17. 11. 1993

Abstract

The karyotype of a female okapi showing 2n = 44 has been investigated by G-R-C and Ag-NOR banding methods. This animal is the offspring of a captive female and a wild-caught male, which are both heterozygotes showing 2n = 45 with centric fusion between two unequal-sized acrocentric chromosomes. The okapi karyotype was arranged according to the cattle standard karyotype in consideration of the high degree of banding homologies found between the two species. The reduction from 2n = 46 to 2 = 45 and 2n = 44 is the result of a Robertsonian translocation involving cattle equivalent chromosomes 4 and 26. Other autosomal rearrangements, like centric fusions and a tandem translocation, as well as structural changes in the X and the Y chromosomes, are tentatively identified. The location of centromeric heterochromatin and of nucleolus organizer regions in the okapi karyotype are described and discussed in relation to the karyotype in other species of Bovidae.

Introduction

The place of the Giraffidae, including the okapi, in the mammalian systematics is still controversial (Gijzen 1959; Taylor et al. 1969; Romer and Parsons 1986). Before the advent of the banding techniques, the chromosomes of the okapi (*Okapia johnstoni*), one of the two surviving species in the family Giraffidae, were first examined by Ulbrich and Schmitt (1969) showing 2n = 46. Subsequently, Hösli and Lang (1970) studied two other animals with 2n = 45. Later Benirschke et al. (1983) confirmed the fusion between two acrocentric autosomes as a common cytogenetic event referred to as "Robertsonian" without phenotypical changes in animals with reduction from 46 to 45 chromosomes. Using various banding methods, Petit and Meurichy (1986) studied two other animals showing 2n = 46 and 2n = 45 in a female and a male okapi, respectively. We were also able to notice the centric fusion between two unequal-sized acrocentrics in the male heterozygote animal with 2n = 45. We report here the cytogenetic studies of a fertile female animal with 2n = 44 (Studbook No 328) showing two translocated elements as the chromosomal origin of her homozygote status and of her male son with 2n = 45 (Studbook No 403), respectively. The okapi "nombre fondamental" (NF) of 60 is very close to the most common bovid NF of 60, therefore, karyotypes of these animals were performed according to standardized cattle banded karyotype (ISCNDA 1989).

Material and methods

Figure 1 illustrates the pedigree prepared from the International Studbook of the Okapi (Puijenbroeck and Bois 1991). Animals No 257 and No 273 were previously reported on by Petit and Meurichy (1986). The diploid chromosome number of okapi No 283 was established in a North-American zoo. To our knowledge, animals No 311 and No 343, have not yet been karyotyped. Chromosome studies of the remaining animals (Studbook Nos 219, 403) were routinely performed by

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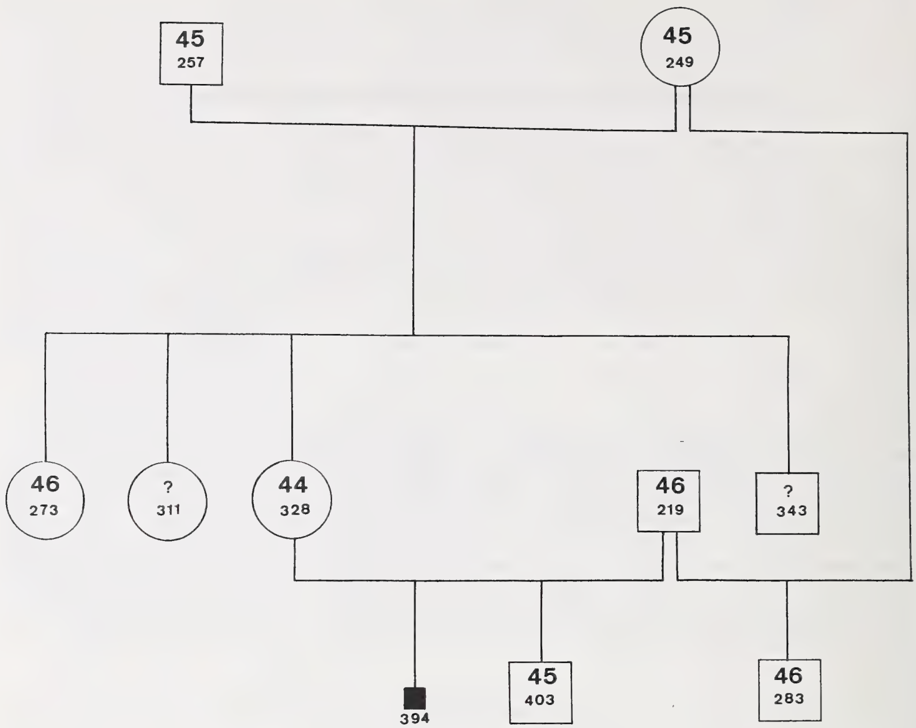

Fig. 1. Pedigree of okapi with studbook numbers in lowercase and chromosome numbers in uppercase. 46 indicates diploid number with absence of t(4;26); 45 and 44 heterozygote and homozygote for t(4;26), respectively indicates male stillborn and ? that chromosome number is unknown

us. The metaphases were observed from cultured skin biopsies, applying to medium and high resolution G and R coloration banding methods (Pai and Thomas 1980; Yunis et al. 1978). C-bands were stained applying to the method of Sumner (1972). Nucleolus Organizer Regions (NORs) have been located using the silver staining technique (Goodpasture and Bloom 1975). The okapi karyotypes were constructed from at least ten well banded metaphase spreads in each case and were prepared according to the standardized cattle banded karyotypes (ISCNDA 1989).

Results

The G-banded karyotypes of two animals demonstrating the reduction from 2n = 45 to 2n = 44 are illustrated in figure 2. In the female with 2n = 44 seven pairs of submetacentric and fourteen pairs of acrocentric chromosomes are numbered according to the cattle nomenclature (ISCNDA 1989). As a consequence of this, the seven biarmed chromosomes are identified as follows: t(27;2;23), t(4;26), t(5;29), t(10;24), t(14;25), t(17;18), t(20;22). The t(27;2;23) is a Robertsonian type 2;23 translocation and 2;27 a tandem translocation. The centromeric region of the chromosome 27, fused at the telomeric region of 2, could not be identified. This t(27;2;23) has been identified previously as t(2;22) by Petit and Meurichy (1992). The translocation event which concerns the chromosomal homozygosity in the 2n = 44 female okapi is identified as t(4;26). The remaining acrocentric okapi chromosomes appear similar in G- and R-banding to the banding patterns of cattle homologues (Fig. 3).

Fig. 2. a: G-bandes karyotype of the 2n = 44 female okapi (Studbook No 328) showing the two t(4;26) elements. b: G-banded karyotype of 2n = 45 male heterozygote (Studbook No 403)

In the male animal with the modal number of 2n = 45 heterozygosity for t(4;26) is demonstrated in figure 2. After using C-banding, small amounts of centromeric heterochromatin (HC) are observed in all the biarmed chromosomes as in t(27;2;23), t(5;29), t(10;24), t(17;18), respectively, whereas in the two remaining translocation elements t(4;26) and t(20;22) much larger HC blocks are demonstrated (Fig. 4). After NOR banding silver dots are observed located in the centromeric region of chromosomes 3, 6, 11, and 28, respectively (Fig. 5).

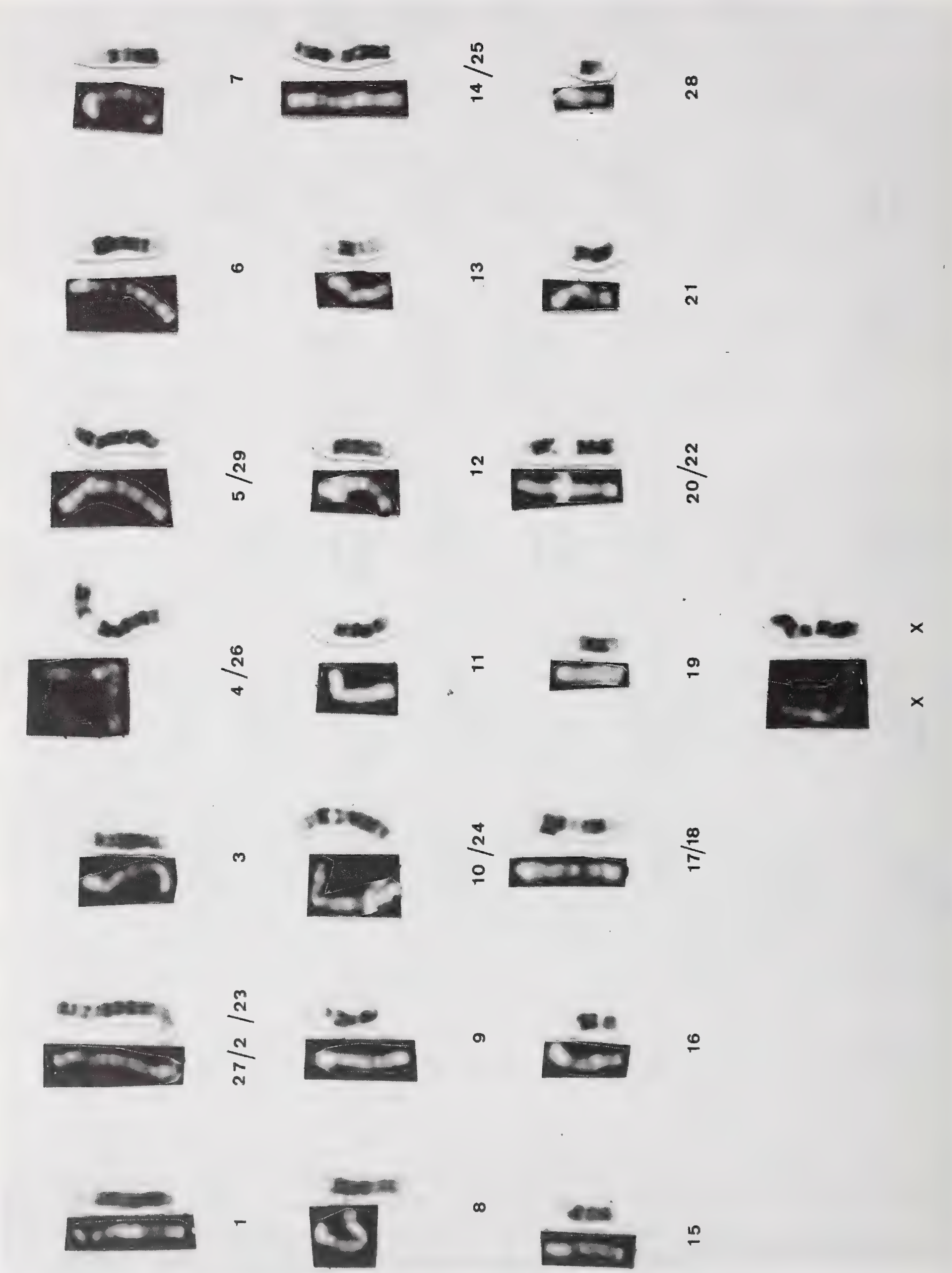

Fig. 3. Combined R-G-banded haploid karyotype of the 2n = 44 animal

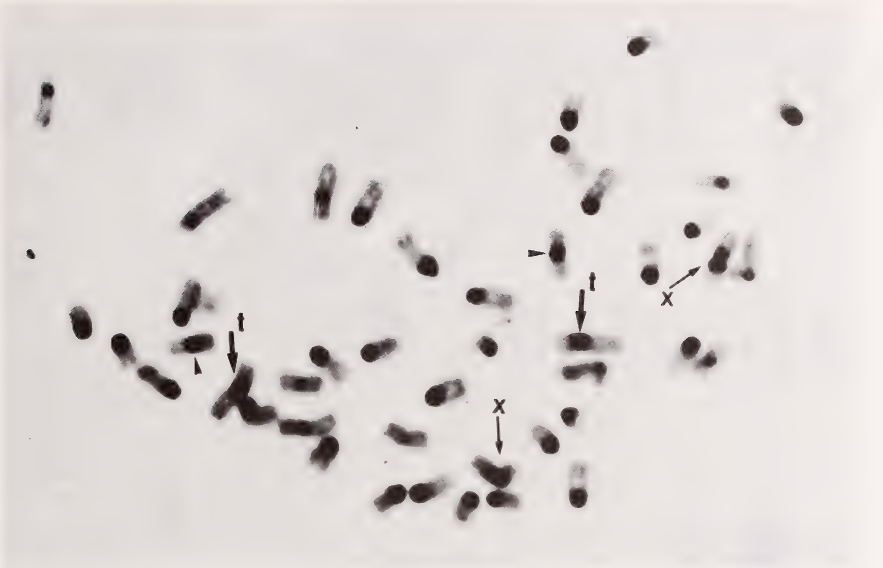

Fig. 4. C-banded metaphase chromosomes of the 2n = 44 animal showing large heterochromatin blocks in two t(4;26) and t(20;22) elements (large arrows: t) and an additional interstitial C-band close to the centromeric C-band in the X chromosomes (small arrows). Note also reduced amounts of HC in the other biarmed chromosomes except for t(4;26) and t(20;22) (arrowheads)

Discussion

From a survey of 21 okapi, Benirschke et al. (1983) reported that 8 animals had 46 chromosomes and 13 had 45 chromosomes. These authors demonstrated that the reduction from 46 to 45 chromosomes was the result of a Robertsonian translocation between two unequal acrocentrics without deleterious effect in the carriers. Recently 43 animals have been karyotyped, among a captive population of 74 animals, showing that 18 animals possess 46 and 25 only 45 chromosomes (Puijenbroeck and Bois 1991). However, the geographical origin of the t(4;26) remains unknown and was most likely imported from the wild as suggested by Benirschke et al. (1983). Thus, the conception of an okapi animal with 2n = 44 resulting from mating of a captive mother (No 249) with a wild-caught father (No 257) would occur at a frequency of 25 % when two 2n = 45 animals are crossed. In this report a 2n = 44 fertile female (No 328) gave birth to a male stillborn (20 kg) with 2n = 45 (No 394) without visceral anomalies at autopsy, and later to a second healthy male (No 403) with 2n = 45. Furthermore, the history of this 2n = 44 female okapi did not reveal either miscarriages or aborted malformed fetuses as a result from chromosomal malsegregation. According to Fosse (1978) neonatal mortality rate in the captive okapi population was high but has been virtually eliminated in the United States in contrast to the European okapi population (Bois et al. 1988).

Cytogenetically, the distribution of HC, as revealed by C-banding, has demonstrated interesting features in the okapi karyotype. At first, the well marked amount of HC in the acrocentric autosomes is conform with observations in cattle (Buckland and Evans 1978b). Secondly, in the pericentromeric regions of the fused elements t(4;26) and t(20;22) large blocks of HC contrast with the small blocks in the 5 other translocated autosomes. Similarly, large blocks of HC on t(15;25) in contrast with a small block on t(1;29), has been

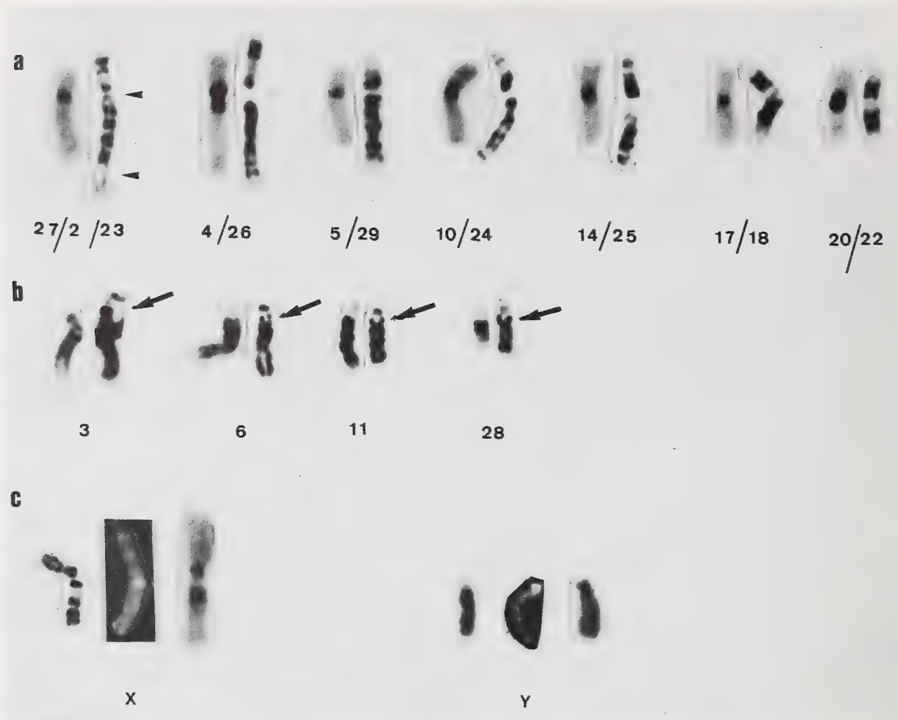

Fig. 5. a: The seven bi-armed okapi chromosomes after C- and G-banding. Arrows indicate the breakpoints in the composite t(27;2;23). b: Acrocentric autosomes 3, 6, 11, and 28 after consecutive G-banding (left) and NOR staining dots (arrows). c: Representative okapi sex chromosomes obtained by G-R-C-banding from left to right

reported in a 59,XX Portuguese Barrosa cow (Iannuzzi et al. 1992). These findings imply that translocated chromosomes, involving fusion of different bovid acrocentric autosomes, may initially contain large blocks of HC which are reduced in size with time. Thus, recent or "new" Robertsonian translocations should progressively loose blocks of HC in the biarmed chromosomes during further evolution.

With regard to the Robertsonian fusions, the presence of the 2;23 translocation in the river buffalo (2n = 50) and in the anoa (2n = 46) was also demonstated but without additional translocated chromosome 27 at the telomeric region of chromosome 2 (Iannuzzi et al. 1990). As a consequence, the resolution of the composite t(27;2;23) characterizes the okapi karyotype. Comparison of the okapi karyotype with a recent cytogenetic survey of 12 bovid species, has indicated considerable monobrachial G-band homologies, but few biarmed chromosome homologies (Gallagher and Womack 1992). Interestingly we have found that the okapi not only shares t(14;25) and t(17;18) with the Roosevelt gazelle (2n = 30) but has the t(20;22) in common with the topi (2n = 36). These findings emphasize that certain biarmed homologies are identical among the translocation events which have arisen independently in three Artiodactyla groups, i.e. the Giraffidae, the Antilopinae and the Alcelaphinae (Buckland and Evans 1978a; Gallagher and Womack 1992). In contrast, no homologous biarmed chromosomes have been observed in a comparative study between the okapi and the giraffe showing 2n = 30 with NF = 58 (Petit and Meurichy 1992). However, the metacentric morphology of the X chromo-

some in these related animals is strikingly different from submetacentric X chromosomes in cattle (Petit and Meurichy 1992; Iannuzzi 1990). The large okapi Y chromosome is similar in size to those of the river buffalo and the anoa (Iannuzzi et al. 1990). From previous studies, heterochromatisation of the okapi long arms is evident after C-banding (Petit and Meurichy 1992). According to Matthews and Reed (1991) the large size of the Y chromosome could be considered as resulting from a class of repeated DNA sequences that is represented in the male bovine genome. This could be related to the phenomenon of acquisition of large amounts of HC material, leading to the morphology of the okapi Y chromosome.

Usually, NORs are observed in telomeric positions in the Bovidae (Mayr et al. 1985; Meo et al. 1991). In contrast, we have identified four acrocentric autosome pairs numbered 3, 6, 11 and 28 demonstrating NORs close to the centromeres. Although pericentromeric location of these NORs have been observed by us in several okapis, it remains unclear why the location of NOR in the okapi is centromeric, while in the Bovidae no other examples have yet been described.

Acknowledgements

We wish to thank Prof. K. Benirschke and Dr. L. Iannuzzi for encouragement and Prof. F. Van Leuven for reading the manuscript.

Zusammenfassung

Chromosomenreduktion in einer Okapi-Familie

Der Karyotyp eines weiblichen Okapi, das 2n = 44 aufwies, wurde mittels der G-R-C und Ag-NOR-Bänderung untersucht. Dieses Tier ist das Resultat einer Paarung zwischen einem aus Tierhaltung stammenden Weibchen und einem in Freiheit aufgewachsenen Männchen, welche beide heterozygot sind und 2n = 45 mit einer zentrischen Fusion zwischen zwei ungleich großen akrozentrischen Chromosomen zeigen. Der Okapi-Karyotyp wurde anhand eines Rinderstandards unter Berücksichtigung des hohen Grades an Bandenhomologie zwischen den beiden Spezies angefertigt. Die Reduktion von 2n = 46 auf 2n = 45 und 2n = 44 ist das Resultat einer Robertson'schen Translokation, die das Rinderäquivalent von Chromosom 4 und 26 einbezieht. Abgesehen von den autosomalen Veränderungen wurden auch Tandemtranslokationen und strukturelle Änderungen bei X- und Y-Chromosomen identifiziert. Die Anordnung von zentromerischen Heterochromatin und Nucleolus organisierenden Regionen im Okapi-Karyotyp werden unter Bezugnahme auf den Karyotyp anderer Arten der Bovidae beschrieben und diskutiert.

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Authors' addresses: P. Petit, M. D., Centre for Human Genetics, U.Z., Gasthuisberg, Herestraat 49, B-3000 Leuven, Belgium; H. De Bois and W. De Meurichy, Royal Zoological Society of Antwerp, Koningin Astridplein 26, B-2018 Antwerpen, Belgium

Z. Säugetierkunde 59 (1994) 161–168

ISSN 0044-3468

Chromosome polymorphism in *Sorex alpinus* (Mammalia, Soricidae) in the western Alps and the Swiss Jura

By E. Dannelid

Institut de Zoologie et d'Ecologie Animale, Université de Lausanne, Lausanne, Switzerland

Receipt of Ms. 19. 7. 1993
Acceptance of Ms. 29. 12. 1993

Abstract

The karyotype (chromosome morphology and G-banding pattern) was examined in 15 individuals of *Sorex alpinus*, the alpine shrew, collected in southwest Switzerland and neighbouring France. All three recorded chromosome numbers, 2N = 58, 56 and 54, occur within Switzerland. It was found that this difference in chromosome number is due to Robertsonian polymorphism. Polymorphism in the number of acrocentric versus subtelocentric chromosomes may also occur.

Introduction

The shrew *Sorex alpinus* is distributed in the mountainous areas of Central and Southern Europe: i.e. the Alps, the Carpathians, the mountains of the western Balkan Peninsula, the Swiss Jura, and some mountainous areas further north in Germany (Schwarzwald, Harz, Fichtelgebirge etc.). There is also one doubtful record for the Pyrenees. The records of distribution are taken from Spitzenberger (1990). Morphologically, *Sorex alpinus* seems to be very distinct from other *Sorex* species and it occupies a rather isolated position within the genus, even though comparisons between *S. alpinus* and the East Asian species *S. mirabilis* have been made. These similarities were mostly due to the shape of the glans penis (Hutterer 1982). Allozyme data also sets *S. alpinus* clearly apart from other *Sorex* species (Catzeflis et al. 1982; Catzeflis 1984).

The karyotype of *Sorex alpinus* is not well known, Reumer and Meylan (1986) give 2N = 54–56 (Catzeflis et al. 1982), 56 (Zima and Král 1984) and 58 (Meylan 1964, 1966). More recently, Zima and Král (1990) again recorded 2N = 56 for the species. This is a higher chromosome number than in any other Eurasian *Sorex* (except for the members of the *Sorex cinereus*-group in extreme northeast Siberia). Also most chromosomes seem to be acrocentric although no definite statement of the NF-number has been made. This karyotype differs greatly from others known in Eurasian shrews. To the author's knowledge no banding of any kind has ever been published on the chromosomes of this species. In the present study a description of the chromosome set of *S. alpinus* (including G-banding) is given.

Material and methods

The material used consisted of 15 shrews (13 from the Swiss and the French Alps, 2 from the Swiss Jura), 6 males and 9 females, trapped between November 1980 and December 1992. For details regarding sites and dates, see figure 1 and table 1. The chromosomes were prepared by the direct method from spleen and bone marrow. Colchicine was applied for a period varying from 45 to 60 minutes. The preparations were left for 3 days, after which they were digested with trypsin, using a modified form of the method described by Seabright (1971). G-banding was performed on 11 of the individuals. The terminology for the chromosomes follows Levan et al. (1964), thus acrocentric chromosomes are termed t1, t2 etc.

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Results

All three reported diploid numbers of chromosomes, 2N = 58, 56 and 54, respectively, were found among the investigated animals. Four animals (all females) had a diploid number of 58 chromosomes. They were trapped in the Swiss Alps, east of Lake Geneva and north of the Rhone Valley, in the cantons Vaud, Valais and Bern (Fig. 1). Three animals (one male and two females) had a diploid number of 56 chromosomes. Two of these animals were trapped in the Swiss Jura, the third in the Swiss Alps southeast of Lake Geneva, in canton Valais, south of the Rhone Valley (Fig. 1). Eight animals (five males and three females) had a diploid number of 54 chromosomes. These animals were trapped in the Swiss and French Alps, south of Lake Geneva (Fig. 1).

Description of the chromosome formula

The 58-karyotype: There was only one pair of large metacentric chromosomes, two pair of medium-sized subtelocentric chromosomes, one pair of small biarmed chromosomes and 24 pairs of acrocentric chromosomes The X-chromosome was a large submetacentric. Since all investigated animals were females, the Y-chromosome was not known. One individual had one acrocentric pair less, but two pairs of small biarmed chromosomes instead of one pair.

The 56-karyotype: This karyotype differed from the 58-type in that there was one additional pair of large metacentric chromosomes and only 22 pairs of acrocentric chromosomes. The Y-chromosome was possibly acrocentric.

The 54-karyotype: This karyotype differed in that there were three pairs of large

Fig. 1. Location of trapping sites for the animals used in the study

Table 1. **Data of the animals used**

IZEA number	Sex	2N	Date of capture	Locality
989	female	56	06. 11. 1980	Bassins, Vaud
999	female	56	15. 07. 1981	Le Vaud, Vaud
3051	female	54	16. 10. 1987	Les Houches, France
3053	male	54	09. 11. 1987	Les Allamands, France
3300	female	58	25. 08. 1988	Bärfel, Oberwald, Valais
3421	male	54	20. 12. 1988	Les Houches, France
3422	female	58	20. 12. 1988	Innertkirchen, Haslital, Bern
3780	male	54	15. 11. 1989	Les Houches, France
4330	male	54	02. 09. 1991	Champéry, Val d'Illiez, Valais
4331	female	54	02. 09. 1991	Champéry, Val d'Illiez, Valais
4705	female	58	09. 09. 1992	Innertkirchen, Haslital, Bern
4709	male	56	21. 09. 1992	Mase, Val d'Hérens, Valais
4710	female	58	01. 10. 1992	Pont-de-Nant, Vaud
4713	male	54	16. 10. 1992	Champéry, Val d'Illiez, Valais
4732	female	54	02. 12. 1992	Les Houches, France

Note: the numbers given for the two first animals are not IZEA-numbers, they refer to a collection made by Francois Catzeflis, and storend at the Institut de Zoologie et d'Ecologie Animale in Lausanne.

biarmed chromosomes (two metacentric and one submetacentric) and only 20 pairs of acrocentric chromosomes. The Y-chromosome was small and probably biarmed.

The G-banding pattern

The G-banded pattern of the chromosomes is shown in figures 2 and 3. The G-banding showed that of the two large metacentric pairs, the one here called m2 was present in all animals. The pair m1 occurred in 54- and 56-animals and was formed by a fusion between the acrocentric chromosomes called t9 and t11 in 58-animals. Finally, the large submetacentric pair (sm1) occurring only in 54-animals was formed by a fusion between the acrocentric pairs called t4 and t20 in other animals. The relative length of the different chromosomes is given in table 2.

Discussion

Robertsonian polymorphism

The different diploid numbers of chromosomes in *Sorex alpinus*, 58, 56 and 54, respectively, were invariably connected with different numbers of large biarmed autosomes (note that the X was also large and biarmed), one pair in the 58-type, two pairs in the 56-type and three pairs in the 54-type. It may be noted that Zima and Král (1990) found 56 chromosomes and that "the female karyotype contained three pairs of large biarmed chromosomes", of which one was obviously the X-chromosome, in *Sorex alpinus* from Czechoslovakia. Thus, it seems highly plausible that the difference in chromosome number within the species is due to Robertsonian translocations.

G-banding analysis confirmed this. Of the three large biarmed pairs of autosomes the pair m2 was present in all animals. The pair m1 was present in 56- and 54-animals and formed by the acrocentric pairs t9 and t11 in 58-animals. The pair sm1 was present only in 54-animals and was formed by the acrocentric pairs t4 and t20 in the other animals.

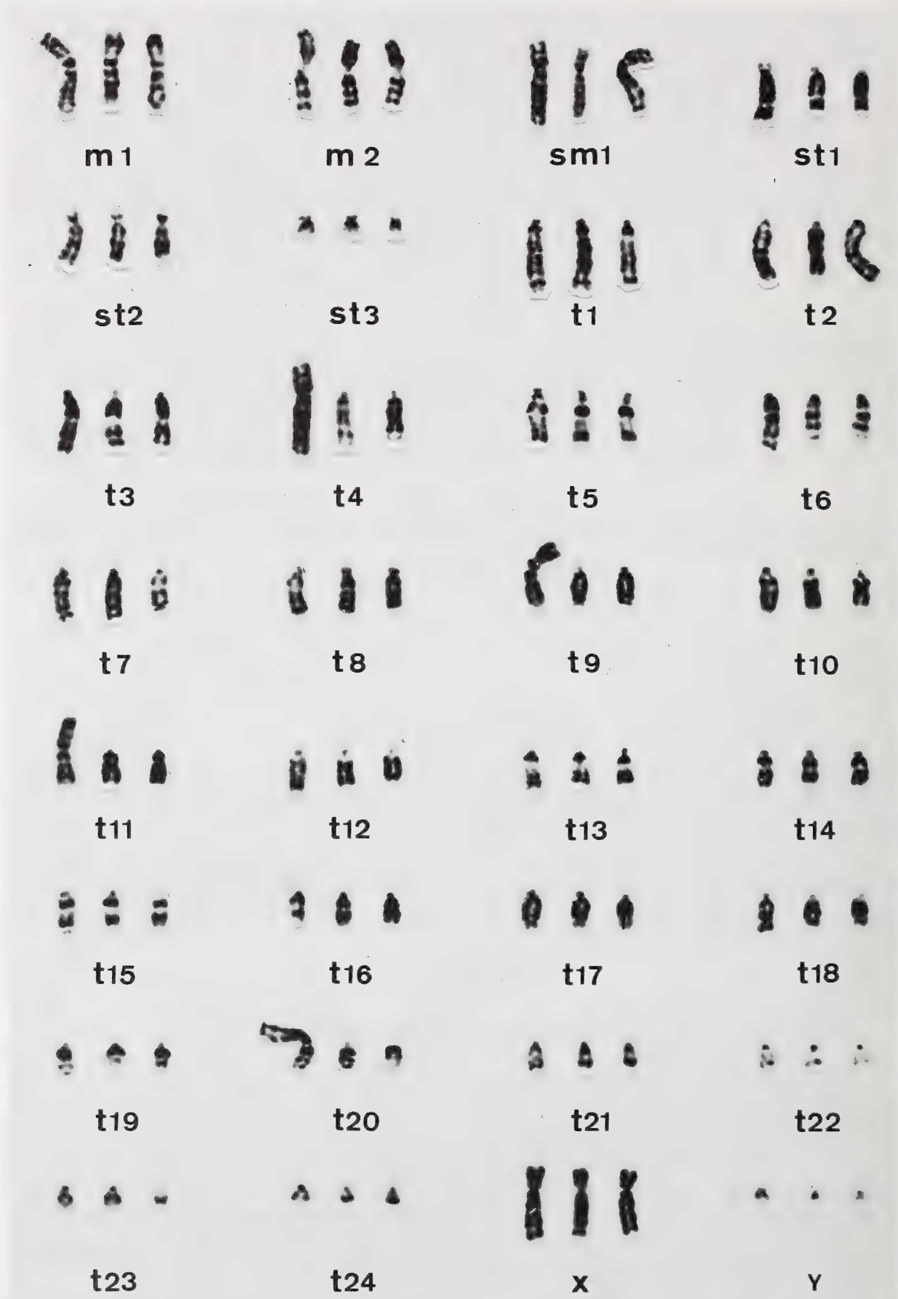

Fig. 2. G-banded chromosomes of *Sorex alpinus*. Three different specimens of each chromosome are shown. For the acrocentric chromosomes involved in Robertsonian fusion, the fusion is also shown

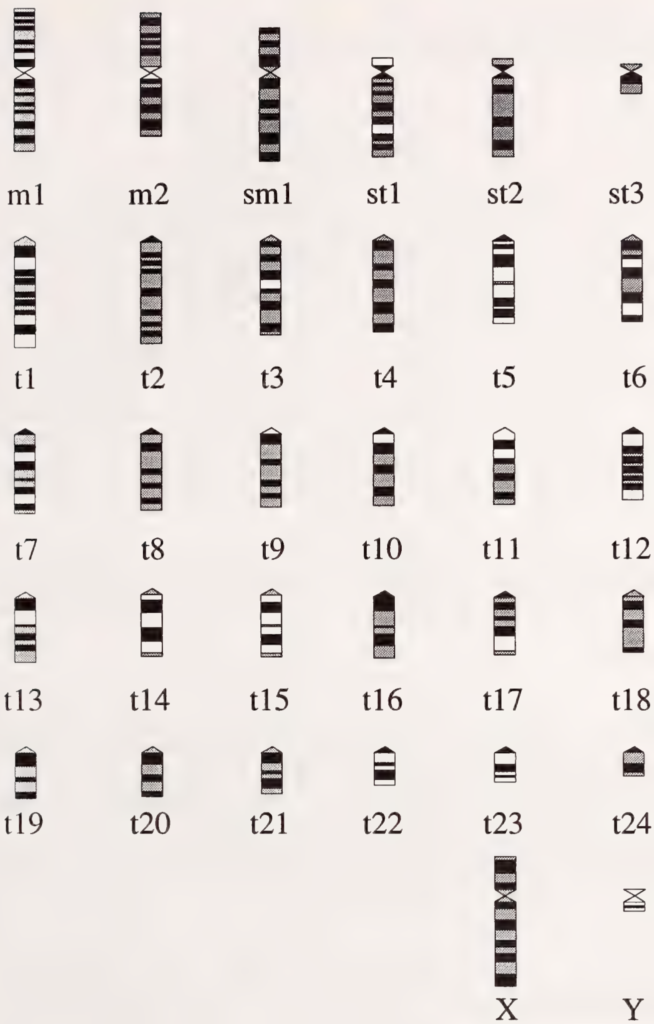

Fig. 3. G-banding pattern of the chromosomes of *Sorex alpinus*

It is generally agreed that in mammals, centric fusion is a much more common process than centric fission. This idea should lead to the hypothesis that the 58-karyotype is the most primitive character state, and that a fusion between pair t9 and pair t11 gave rise to the 56-karyotype. Another fusion, this time between pair t4 and pair t20 led to the 54-karyotype.

The material examined in this study is probably too small in number to determine whether the variation in chromosomal number is geographically correlated (as seems probable). However, at least the 54-karyotype seems to have a specific geographical distribution. It was the most frequently encountered, eight animals, all captured in an area south of Lake Geneva (chiefly Les Houches in French Savoia and Val d'Illiez in canton Valais) where all animals had the 54-karyotype.

The 58-karyotype was encountered in animal east of Lake Geneva, from Haslital in

Table 2. **Length of chromosome arms**
(in mean percentage of length of female haploid set)

	Shorter arm	Longer arm	Total
m1	3.43	3.52	6.95
m2	2.86	3.00	5.86
sm1	2.11	4.42	6.53
st1	0.52	3.50	4.02
st2	0.48	3.53	4.01
st3	0.36	1.02	1.38
t1			5.52
t2			5.22
t3			5.18
t4			4.55
t5			4.45
t6			4.35
t7			3.95
t8			3.88
t9			3.55
t10			3.55
t11			3.37
t12			3.19
t13			3.16
t14			3.16
t15			2.97
t16			2.93
t17			2.87
t18			2.85
t19			2.30
t20			2.25
t21			2.17
t22			1.69
t23			1.52
t24			1.37
X	1.89	4.03	5.92
Y			0.62

canton Bern in the north to Pont-de-Nant in canton Vaud in the south- and east to Bärfel, Oberwald in canton Valais. These localities were all situated north of the Rhone Valley. The sample consisted, however, of only four individuals.

The 56-karyotype, finally, presents some problems. Of the three individuals, two were captured in the Swiss Jura, north of Lake Geneva, while the third was from Val d'Hérens in canton Valais, which is south of the area with 58-animals. Finally, it exists in Czechoslovakia (Zima and Král 1990). It may be noted that the material analysed by Zima and Král (1990) originated from two geographically isolated distribution areas, in the Carpathians in Slovakia and in the Jeseníky Mountains in Czechia.

Previous results from Meylan (pers. comm.) seem to indicate that neither the distribution of the 54-karyotype nor that of the 58-karyotype is geographically homogeneous.

However, the data in this study suggest that the distribution of the three different karyotypes is geographically correlated, and assuming this to be true, two alternative hypotheses may be formed.

The first hypothesis is that the 58-karyotype is the most ancient and via centric fusions has given rise to the 56- and 54-karyotypes, as suggested above. In this case the original 58-karyotype has been replaced by the 56-karyotype south of the Rhone and further westward (and northeastward). The 54-karyotype then arose from the 56-karyotype in the area south of Lake Geneva, thus separating the 56-populations of the Jura from those of the Alps.

The second hypothesis takes into account the large and nonhomogeneous distribution of the 56-karyotype. However, genetically it seems to be constant. By studying banded material from western Czechia (Sumava mountains) it was possible to confirm that the fusion of t9 and t11 into m1 is the same there as in the Jura and in Valais south of the Rhone Valley. This hypothesis should thus be that the 56-karyotype is the most ancient, and has given rise to the 54-karyotype (via centric fusion) and to the 58-karyotype (via centric fission).

It would be interesting to compare these karyological data with differences in morphology and electrophoresis from the different areas. Unfortunately, very few publications have been concerned with *Sorex alpinus*. Catzeflis et al. (1982) found electrophoretic polymorphism in this species (6 loci out of 17 studied); all their individuals were, however, from one locality (Pont-de-Nant in canton Vaud). Moreover, Catzeflis (1984) again reported polymorphism in *Sorex alpinus*; animals from Pont-de-Nant (which should have

the 58-karyotype) had 5 polymorph loci (out of 35 studied), while in animals from the Swiss Jura (which should have the 56-karyotype) only one polymorph locus (not polymorph in Pont-de-Nant) was found.

Other polymorphies

ZIMA and KRÁL (1990) recognized two pairs of subtelocentric chromosomes in this species. Actually, there are probably more than two pairs of subtelocentrics (excluding the tiny st3). In some Giemsa-stained preparations up to six could be distinguished. In some metaphases almost all autosomes appeared to be biarmed, and ZIMA recorded the same condition for the Czechoslovakian material (ZIMA, pers. comm.). However, only pairs st1 and st2 (in size order corresponding closely to the two pairs described by ZIMA and KRÁL (1990) and thus probably identical with these) were easily recognized, moreover, these two pairs were the only ones possible to identify as subtelocentrics also in the G-banding. The other chromosomes sometimes appearing as subtelocentrics quite as often were acrocentric. This non-constant condition might be due to centromeric shift, or to different interpretation because the smaller arms are sometimes exceedingly difficult to see, especially if the chromosome is in a contracted state. A possible third subtelocentric pair might be the pair here termed t8.

To ascertain whether the distribution of the 58-, the 56-, and the 54-karyotypes is geographically correlated and in that case to determine the distributions greater detail, further studies on the karyology on this species are needed, also from other parts of its distributional area.

Acknowledgements

The author wishes to express his gratitude to ANNE-MARIE MEHMETI for help with the preparation of the chromosomes. I am also grateful to Prof. PETER VOGEL, HARALD BRÜNNER and LUCA FUMAGALLI for bringing me shrews when my own trapping success was declining. I am indebted to Prof. JACQUES HAUSSER, Lausanne, Prof. EDWARD FARMER, Lausanne, Prof. BO FERNHOLM, Stockholm, Prof. KARL FREDGA, Uppsala and Dr. JAN ZIMA, Brno for critical comments on the manuscript. Finally, I wish to thank the Swedish Institute, Wallenbergsstiftelsens jubileumsfond, A. F. Regnells Zoologiska gåvomedel, Helge Ax:son Johnsons stiftelse, Hierta-Retzius fond för vetenskapling forskning and Stiftelsen Wenner-Gren Center for the financial supply that made this work possible.

Zusammenfassung

Chromosomenpolymorphismus von Sorex alpinus (Mammalia, Soricidae) in den Westalpen und im Schweizer Jura

Der Karyotyp von *Sorex alpinus* wurde für 15 Tiere anhand der Chromosomenmorphologie und des G-Bandenmusters analysiert. Alle drei bisher bekannten Chromosomenzahlen 2n = 58, 56 und 54 wurden für die Schweiz nachgewiesen. Ebenso konnte gezeigt werden, daß der Unterschied in der Chromosomenzahl durch einen Robertsonischen Polymorphismus bedingt wird.

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Author's address: Erland Dannelid, Department of Zoology, Stockholm University, S-106 91 Stockholm, Sweden

Z. Säugetierkunde 59 (1994) 169–173

ISSN 0044-3468

Placental scar counts in the Red fox (*Vulpes vulpes* L.) revisited

By E. R. Lindström

Grimsö Wildlife Research Station, Department of Wildlife Ecology, Swedish University of Agricultural Sciences, Sweden

Receipt of Ms. 8. 7. 1993
Acceptance of Ms. 28. 2. 1994

Abstract

Placental scars used for analyses of reproduction in the red fox (*Vulpes vulpes* L.) may fade throughout the season after birth. I report a method to calculate whelping frequency and mean litter size from placental scar analyses of 608 vixens shot during autumn and winter in three areas of Sweden. The material allowed 6-9 consecutive periods of calculation within the year in each area. By successively including scars of lighter shades in the counts, I established isopleths of constant whelping frequencies. The isopleth yielding the best estimate of mean litter size as derived from analyses of vixens in late pregnancy was accepted for calculations in each area. Although this method appeared to be adequate for each area, there were inter area differences. Therefore, reference material is needed for each specific area before this method can be used.

Introduction

Placental scars provide convenient measures of litter size and whelping frequency (proportion of females that give birth) in the red fox (*Vulpes vulpes* L.), and the method has been applied extensively (e.g. Sheldon 1949; Richards and Hine 1953; Layne and McKeon 1956; McIntosh 1963; Wandeler 1968; Fairley 1970; Englund 1970; Wandeler et al. 1974; Ryan 1976; Storm et al. 1976; Ulbrich 1977; Pils and Martin 1978; Kolb and Hewson 1980; Artois et al. 1982; Allen 1983; Harris and Smith 1987; Lindström 1988, 1989, 1992; Ansorge 1990). However, different shades of scars may originate at resorption sites, be persisting from old pregnancies or from cubs born the previous spring (Englund 1970). Hence, Englund (1970) based his calculations on the darkest scars only. Lindström (1981) showed that the shade of a scar may fade throughout the year following birth. Accordingly, I modified the method to account also for the fading, and in such a way that the scars of 4 vixens with known minimum litter sizes were correctly interpreted (Lindström 1981). Here, I report a new attempt to determine which scars should be counted at different intervals after birth, including new material and with a new approach.

Material and methods

Placental scars were counted in adult (≥ 1 year) vixens that showed no sign of fresh ovulation (an indication of a new pregnancy). The carcasses were collected from hunters in three parts of Sweden: Västerbotten (approximately 65 °N, 20 °E, n = 203, 1982–1990), Bergslagen (approximately 60 °N, 15 °E, n = 284, 1975–1990), and Småland (approximately 57 °N, 15 °E, n = 121, 1983–1990). The hunting season, i.e. the season of collection, lasted from early August to mid-March/mid-April (depending on area). Adult age was indicated by epiphyseal closure of the tibia. Placental scars were classified by shade of darkness from 1 (hardly visible) to 6 (completely black).

An additional 30 pregnant vixens with fetuses of a crown-rump length > 12 mm (i.e. at least halfway through pregnancy, see e.g. Englund 1970) were used for calculating mean litter size. For comparison of mean litter sizes, I used 95 % confidence intervals.

The exact date of death of the fox was not known in all cases. Hence, the week numbers were used

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as the time base; a year encompasses weeks 1–52 except every 5th or 6th year, which also includes week no. 53.

Mean litter size and whelping frequency were calculated for scars of shade 6, shade 6 + 5, shade 6 + 5 + 4, etc. until scars of all shades were included. This was done for consecutive periods throughout the season of collection in each area. At least 20 individuals were desired for each period, but especially in early autumn and late winter, this number was not possible to attain. The shades that had to be included during the different periods to obtain isopleths of constant whelping frequencies (40, 50, 60 and 70 %) throughout the season were noted, and the resulting mean litter size was calculated for each isopleth. This was then compared with the mean litter size as calculated from pregnant vixens and the isopleth giving the best fit was chosen for each area. To make a final adjustment I also checked the chosen isopleths for the best estimates of the mean litter size during each consecutive period.

Results and discussion

Mean litter size in late pregnancy

Mean embryonic litter size did not differ statistically among areas (means ± 95 % confidence intervals: Västerbotten 5.7 ± 1.2, n = 9; Bergslagen 5.1 ± 0.89, n = 15; and Småland 4.8 ± 1.6, n = 6). Thus, I pooled the materials and calculated an overall average of 5.2 ± 0.58 cubs. The confidence interval thus obtained covered the average of 4.8 cubs per litter (n = 489) noted by Englund (1970) in his total material of pregnant vixens from four areas of Sweden.

In five comparisons, embryo counts overestimated mean litter size as calculated from cubs at dens by an average of 18.5 % [range 0-63 %; data from McIntosh (1963); Wandeler et al. (1974); Storm et al. (1976); Pitzschke (1972) combined with Stubbe and Stubbe (1977); Pils and Martin (1978)]. Appling this figure to Englund's (1970) data would yield 4.1 cubs at dens. For different reasons, embryo counts are likely to overestimate the number born, whereas counts of cubs at dens are subject to the opposite. I have used a tentative estimate of 4.5 cubs born per litter in all three areas.

Selecting isopleths

The results did not vary much when scars of all shades were included in the calculations (Tab. 1). However, the darkest scars were primarily found early in the season. Thus, although dark scars faded, no scars seemed to disappear completely within one season.

Isopleths of constant whelping frequencies could be established by successively including scars of lighter shades (Tab. 1), and the corresponding mean litter sizes were calculated (Tab. 2). In Västerbotten the best estimate of the mean 4.5 cubs born was attained by the 60 % isopleth, whereas the 70 % isopleths yielded the best fits in Bergslagen and Småland.

Adjustments to obtain the best fit of mean litter size in single time periods yielded the finally accepted trajectories (series) of successive shades to be included in the counts: (shades counted early in autumn; subsequently included shade/week when first included) Västerbotten 6–4; 3/46; 2/5, Bergslagen 6–4; 3/41; 2/52, Småland 6–3; 2/1.

All previously counted scars were included in the new counts, but 22 % of the vixens with accepted scars had an increased number of scars as compared with the old method. Half of these vixens were previously considered as having had no cubs. The number of scars now counted in the uteri of the four vixens with known minimum (!) litter sizes (Lindström 1981) overestimated these by 1–3 cubs.

The series of shades to be successively considered in the scar counts presented above should not be applied in any other areas. However, the method of calculating these provides a possibility to analyze fading of the scars whenever a material large enough is available, and also to correct for fading if an independent estimate of mean litter size can be obtained. There is no limitation concerning species as long as the method of placental scar

Table 1. **Mean litter size and percent whelping females (left and right of slash, respectively) as calculated from placental scars of increasingly lighter shade and throughout the season of collection (week number 31–13) in Västerbotten (a), Bergslagen (b), and Småland (c)**

Periods indicated by vertical bars. Sample size indicated at the top of each data set

a.

Week	31–45	46–49	50–53	1–2	3–4	5–6	7–8	9–13
n	12	25	40	29	23	27	20	27
shade 6	2.0/ 8	1.0/ 4	3.0/ 3	-/ 0	-/ 0	-/ 0	-/ 0	-/ 0
5-6	5.0/25	2.0/12	2.0/10	-/ 0	4.0/ 4	6.0/ 4	-/ 0	-/ 0
4-6	5.2/42	2.3/56	3.1/30	1.7/10	3.8/22	3.0/19	2.3/15	-/ 0
3-6	6.1/58	4.1/60	4.2/48	2.4/55	3.9/35	3.8/37	3.4/35	3.0/ 4
2-6	6.4/83	5.7/68	5.1/80	4.9/86	5.2/83	5.0/85	5.8/70	5.5/74
1-6	5.8/83	5.3/80	5.4/85	5.5/86	5.5/91	5.5/85	6.0/80	5.2/96

b.

Week	31–40	41–45	46–47	48–49	50–51	52–53	1–2	3–4	5–6	7–8	9–13
n	24	22	24	21	40	17	35	38	27	26	10
shade 6	3.7/38	3.0/18	2.0/13	-/ 0	3.0/15	-/ 0	-/ 0	1.5/ 5	1.0/ 4	-/ 0	-/ 0
5-6	4.3/63	3.5/50	2.6/21	2.5/19	3.7/28	1.0/12	1.8/11	2.0/ 8	1.8/15	2.3/12	1.5/20
4-6	4.9/71	4.2/59	3.1/54	2.6/38	3.7/48	2.6/29	2.1/26	1.9/21	2.7/37	1.8/23	3.0/30
3-6	5.3/75	4.2/77	4.1/79	3.5/71	4.8/58	3.1/47	2.5/51	2.9/50	3.4/63	2.2/50	3.1/70
2-6	5.3/88	5.2/82	4.6/96	5.8/75	5.5/73	5.2/65	4.0/83	4.1/84	4.7/85	4.4/77	5.6/70
1-6	5.7/88	5.7/86	5.0/96	6.8/91	6.1/75	5.3/76	5.0/89	5.0/87	5.5/89	5.3/77	6.3/70

c.

Week	41–49	50–53	1–2	3–4	5–6	7–13
n	16	28	22	21	10	24
shade 6	-/ 0	3.0/ 7	-/ 0	-/ 0	-/ 0	-/ 0
5-6	1.0/ 6	3.5/14	2.0/ 9	-/ 0	-/ 0	-/ 0
4-6	2.8/31	3.2/36	2.6/32	3.8/19	1.0/10	3.0/ 8
3-6	3.8/56	4.0/61	3.7/45	4.3/43	3.0/30	2.7/ 38
2-6	5.3/94	5.1/75	4.5/77	4.7/86	4.3/80	4.1/75
1-6	5.7/64	5.7/79	5.4/82	4.7/95	4.2/90	4.1/92

Table 2. **Mean litter sizes as calculated from the isopleths of 40, 50, 60, and 70 % whelping frequencies in Västerbotten, Bergslagen, and Småland**

Whelping frequency	Mean litter size		
	Västerbotten	Bergslagen	Småland
40	3.8	3.1	3.4
50	3.8	3.1	3.7
60	4.6	3.5	4.0
70	5.3	4.5	4.4

counts is valid. The only assumption needed is that the uteri collected during each subperiod provide an unbiased sample from the population of females alive previous spring.

Acknowledgements

Special thanks go to YLVA LINDROOTH and CHRISTINA LINDSTRÖM for doing the necropsies and the accompanying analyses. Critique and support were offered by JON SWENSON. He also corrected my English language. CHRISTINA LINDSTRÖM, EGON NILSSON, JAN and BIRGIT ÅBERG organized the collection of carcasses. I am also in debt to all hunters who provided the raw material of the study. ANDREAS SEILER helped me with the Zusammenfassung. The study was an integrated part of the environmental monitoring program (PMK) of the Swedish Environmental Protection Agency.

Zusammenfassung

Zählungen von Implantationsnarben beim Rotfuchs (Vulpes vulpes L.), eine Revision

Die Wurfgröße und Wurfhäufigkeit von Säugern mit einer Placenta zonaria können über Implantationsnarben im Endometrium ermittelt werden. Beim Rotfuchs (*Vulpes vulpes* L.) verblassen die Narben jedoch nach erfolgter Geburt. Hier präsentiere ich eine revidierte Methode zur Feststellung, welche Färbungsgrade berücksichtigt werden sollten, um eine korrekte Schätzung der Reproduktion zu verschiedenen Zeitpunkten zu erhalten. Diese Methode basiert auf sukzessiven Berechnungen von Narbenanzahlen unterschiedlicher Intensität. Die Narben, welche die besten Übereinstimmungen mit den beobachteten Durchschnittswurfgrößen ergaben, wurden für jährliche Reproduktionsanalysen bei schwedischen Füchsen verwendet.

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Author's address: Ph. D. Erik R. Lindström, Grimsö Wildlife Research Station, S-730 91 Riddarhyttan, Sweden

Z. Säugetierkunde 59 (1994) 174–180

ISSN 0044-3468

Zur Reproduktionsleistung des Alpensteinbockes (*Capra i. ibex* L.) in der Freilandkolonie Albris (Graubünden, Schweiz)

Von M. Giacometti und P. Ratti

Forschungsinstitut für Wildtierkunde und Ökologie der Veterinärmedizinischen Universität Wien, Österreich, und Jagd- und Fischereiinspektorat des Kantons Graubünden, Schweiz

Eingang des Ms. 13. 12. 1993
Annahme des Ms. 22. 4. 1994

Abstract

On the reproductive performance of the free-ranging alpine ibex population (Capra i. ibex L.) at Albris (Grisons, Switzerland)

In order to evaluate the reproductive performance of alpine ibex (*Capra i. ibex* L.), the uteri and ovaries of 80 females were investigated. The animals came from the colony at Albris (Grisons, Switzerland) and samples were collected during the months December to June in 1989–1990 and 1990–1991.

The females conceived between December 1 and January 21. The earliest age of females to conceive was 2 years with a conception rate of 0.13. Conception rate in 3 year old females was 0.56 and of 4 year old females 1.00. Gravidity rate amounted to 0.88. For 70 females older than 2 years 48 viable embryos could be determined (fecundity rate = 0.69). For the age class 4–13 years fecundity rate equalled 0.83. At 14 years of age a probably age dependent decrease of fecundity was observed (fecundity rate of females 14–16 years old = 0.40). Among 59 mature females 48 viable embryos were found (natality 0.81) and fertility was 0.25. Twins were observed in only 1 out of 52 cases investigated. The reproductive performance detected in this study clearly surpasses the one previously described for this population, which is approaching the carrying capacity of its habitat.

Einleitung

Eine wesentliche Voraussetzung zum Verständnis der Populationsdynamik einer Wildwiederkäuerart ist die Kenntnis der Fertilität, d. h. der in einem Jahr erzeugten Nachkommenzahl einer Population (vgl. Schwerdtfeger 1978). Die Beurteilung der Fortpflanzungsleistung ist aber auch für die Bewirtschaftung freilebender Wildtiere, zum Beispiel von Alpensteinbockpopulationen, von besonderer Bedeutung. In der Schweiz, im Fürstentum Liechtenstein, in Österreich, in Deutschland und in Slowenien (Giacometti 1991) sowie in Südtirol werden zahlreiche Steinbockkolonien zur Regulierung der Bestände jagdlich genutzt.

Die beim Alpensteinbock diesbezüglich vorliegenden Angaben beziehen sich ausschließlich auf die Beurteilung der Anzahl der im Anschluß an die Setzperiode zählbaren Kitze (vgl. Couturier 1962; Nievergelt 1966a; Ratti 1981; Peracino und Bassano 1990). Als Methode diente dabei die Direktbeobachtung. Bei dieser Methode wird aber die peri- und postnatale Kitzmortalität, die hinsichtlich der Gesamtmortalität eine wesentliche Rolle spielt, nicht berücksichtigt (vgl. Heptner et al. 1966; Schröder 1971; Mitchell et al. 1977; Salzmann 1977; Ellenberg 1978; Hofmann 1990; Ballard et al. 1991; Kurt 1991). Es muß somit davon ausgegangen werden, daß die Fortpflanzungsleistung des Alpensteinbockes in freier Wildbahn größer ist als bisher angenommen.

Um diese Hypothese zu prüfen, wurden in der vorliegenden Arbeit die Ergebnisse einer zweijährigen Untersuchung über die Fortpflanzungsleistung des Alpensteinbockes der Freilandkolonie Albris im Kanton Graubünden (Schweiz) ausgewertet; Teilaspekte wurden an anderer Stelle publiziert (Tataruch et al. 1991; Weiss et al. 1993).

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Material und Methode

Von 80 Geißen wurden Uteri und Ovarien untersucht. Die Geißen wurden in den Monaten Dezember bis Juni der Jahre 1989–1990 und 1990–1991 von Wildhütern und Jagdaufsehern im Rahmen eines Sonderabschusses erlegt. Die Tiere stammen von der im Südosten des Kantons Graubünden liegenden Steinbockkolonie Albris. Der dortige Steinwildlebensraum liegt zwischen 1600 und 3200 m Seehöhe. Mit einem gezählten Frühjahrsbestand von 1667 Tieren im Jahre 1990 ist die Kolonie Albris die zahlenmäßig stärkste des Kantons. Im Wintereinstand beträgt die Dichte derzeit etwa 50, jene im Sommereinstand etwa 15 Steinböcke pro 100 ha.

Unmittelbar nach dem Erlegen der Geißen wurden Ovarien und Uteri in Polyethylensäcke verpackt und bis zur Analyse bei −18 °C aufbewahrt. Die Untersuchung erstreckte sich auf die Anzahl, das Geschlecht, das Gewicht und die Entwicklungsfähigkeit der Keimlinge sowie die Anzahl und den Maximaldurchmesser der Corpora lutea. Zur Zählung der Corpora lutea und zur Messung ihres Maximaldurchmessers wurden die Ovarien im frisch aufgetauten Zustand in Scheiben von 0,5 bis 1 mm Dicke geschnitten. Dann wurde eine Scheibe nach der anderen aufgeklappt, hierbei die vorhandenen Gelbkörper gezählt und deren Durchmesser auf einen Millimeter genau gemessen. Das Keimlingsalter wurde nach Hugget und Widdas (1951) berechnet. Dabei wurde eine Trächtigkeitsdauer von 167 Tagen (Stüwe und Grodinsky 1987) und eine tierartspezifische Fetus-Wachstumskonstante a von 0,103 angenommen. Das nach Ratti und Habermehl (1977) aufgrund von Merkmalen am Gehörn bestimmte Alter der Geißen wurde in ganzen Zahlen angegeben, wobei die Periode der vorangegangenen Brunft, unabhängig vom Erlegungsdatum, als Stichzeitpunkt angenommen wurde. Zur Feststellung, ob eine Trächtigkeit vorlag oder nicht, wurden nur jene Geißen berücksichtigt, die nach dem 1. Februar erlegt wurden, und diejenigen, die nachweislich trächtig waren (Keimling vorhanden). Der früheste Zeitpunkt war in diesem Zusammenhang der 11. Januar.

Ergebnisse

Gelbkörperrate und Gelbkörperdurchmesser

Die Gelbkörperrate (Anzahl der Corpora lutea periodica und graviditatis bezogen auf die Anzahl reproduktiver Geißen) betrug 1,05 (n = 55) (Geißen, die bereits gesetzt hatten oder bei welchen eine pathologische Gravidität festgestellt wurde, blieben unberücksichtigt). Bei trächtigen Steingeißen war in den Monaten Februar bis Juni die Zahl der Corpora lutea graviditatis mit jener der Keimlinge identisch (n = 34). Der Maximaldurchmesser der Corpora lutea graviditatis beträgt durchschnittlich 14,8 mm (n = 35, s = 2,2); er nimmt bei fortschreitender Trächtigkeitsdauer an Größe zu ($r^2 = 0{,}655$, $p < 0.001$).

Konzeptionszeitpunkt

Die Konzeption erfolgte in der Zeit zwischen dem 1. Dezember und dem 21. Januar (n = 37) (vgl. Abb. 1); 86,5 % der Geißen konzipierte zwischen dem 6. und dem 29. Dezember, somit innerhalb einer Zeitspanne von 23 Tagen. Der mittlere Zeitpunkt, an welchem die Geißen konzipierten, war der 19. Dezember.

Geschlechtsreife und Konzeptionsraten

Die Geißen der Kolonie Albris konzipierten frühestens im Alter von 2 Jahren. Die Konzeptionsrate der 2jährigen Geißen (Anzahl der entwicklungsfähigen und abgestorbenen Keimlinge bei Geißen einer bestimmten Altersstufe oder -klasse bezogen auf die Anzahl Geißen derselben Altersstufe oder -klasse) betrug 0,13 (n = 8). Die Konzeptionsrate der 3jährigen Geißen lag bei 0,56 (n = 9), jene der 4jährigen bei 1,00 (n = 9).

Trächtigkeitsrate

Von allen geschlechtsreifen Geißen (n = 59) waren 52 trächtig, was eine Trächtigkeitsrate von 0,88 ergibt.

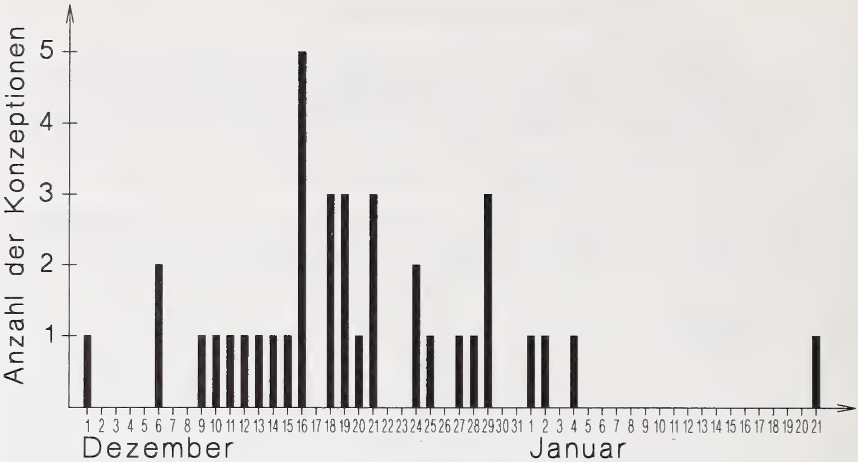

Abb. 1. Konzeptionszeitpunkt bei den Steingeißen der Kolonie Albris (n = 37)

Pränatale Mortalität

In fünf von 52 Fällen wurde eine pathologische Gravidität festgestellt (2 Fälle im Resorbtionsstadium, 2 Frühaborte, 1 Mumifikation). Die pränatale Mortalität beträgt demnach 9,6 %. Aufgrund ihres Verhaltens intra vitam und des Sektionsbefundes können die Geißen als gesund beurteilt werden. Bei einer Geiß wurde jedoch serologisch ein Titer von 1 : 100 gegen *Leptospira bratislava* (Geiß Nr. 579), bei der Geiß Nr. 593 ein Titer von 1 : 16 gegen *Chlamydia psittaci* festgestellt. Mißgebildete Feten wurden nicht festgestellt.

Ausgewählte Fekunditätsraten beim Alpensteinbock der Kolonie Albris

Altersklasse (Jahre)	Fekunditäts-rate	n
0– 1	0,00	10
2	0,13	8
3	0,56	9
4–13	0,83	48
14–16	0,40	5
3–13	0,79	57
1–15	0,63	76

Fekunditätsraten

Ausgewählte Fekunditätsraten (im Sinne von Asdell 1946; Andrewartha et al. 1954; Nievergelt 1966a) sind aus der Tabelle und in Abb. 2 ersichtlich (bei den Fekunditätsraten wird, im Gegensatz zu den Konzeptionsraten, nur die Anzahl entwicklungsfähiger Keimlinge berücksichtigt). Die für die Berechnung der Fertilität herangezogene und deshalb besonders bedeutsame Fekunditätsrate der 2jährigen und älteren Geißen beträgt 0,69 (n = 70).

Potentielle Natalität

Bei den 59 reproduktiven Geißen konnten insgesamt 48 sich bildende, entwicklungsfähige Keimlinge nachgewiesen werden. Das ergibt eine potentielle Natalität (im Sinne von Schwerdtfeger 1978) von 0,81. In Abb. 3 sind die Gelbkörperrate, die Trächtigkeitsrate und die potentielle Natalität dargestellt. Die potentielle Natalität beträgt 77,1 % der Gelbkörperrate.

Fertilität

Als Fertilität wird nach Schwerdtfeger (1978) die Zahl der Nachkommen bezogen auf 1 Individuum einer Population (Tiere aller Geschlechts- und Altersklassen) verstanden.

Ausgehend von der oben angeführten Fekunditätsrate der 2jährigen und älteren Geißen (0,69) und von den in der Kolonie Albris im Frühjahr 1990 und 1991 gezählten Steinböcken (3211 Tiere, davon 1185 Geißen von 3 und mehr Jahren) kann eine Fertilität von 0,25 berechnet werden.

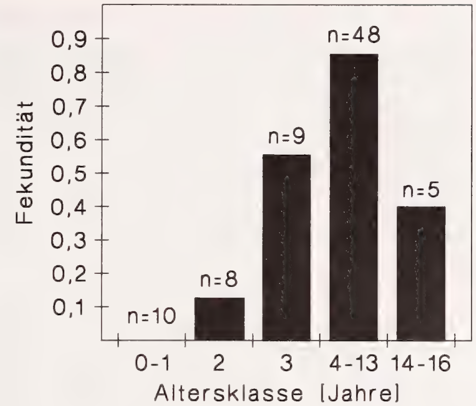

Abb. 2. Fekunditätsraten von 5 ausgewählten Altersklassen

Satzgröße und Geschlechterverhältnis

Einzig bei einer 5jährigen Geiß waren Zwillinge nachzuweisen. Alle anderen Geißen waren unipar, die Häufigkeit der Zwillingsträchtigkeiten betrug 1,9 %. Das Geschlechterverhältnis (Weibchen zu Männchen) der ungeborenen Kitze betrug 1:1,21 (n = 31).

Diskussion

Bisher liegen keine Angaben zu Gelbkörperraten und zum Gelbkörperdurchmesser beim Alpensteinbock vor. Bei anderen Caprinae (z. B. Valentinčič et al. 1974; Bauer 1972; Kita et al. 1987) und bei Cerviden (z. B. Valentinčič 1958; Wandeler 1975; Buchli 1979; Schwartz et al. 1993) sind hingegen Zählungen von Corpora lutea zur Bestimmung der Ovulationsrate durchgeführt worden. Die Tatsache, daß die potentielle Natalität lediglich 77,1 % der Gelbkörperrate beträgt, zeigt, daß auch beim Alpensteinbock die während der Brunftzeit ermittelte Gelbkörperrate sich nicht zur Beurteilung der Natalität eignet (vgl. Hofmann 1990). Makroskopisch lassen sich Corpora lutea periodica und Corpora lutea graviditatis nicht sicher unterscheiden (Salzmann 1977). Beim Serau (*Capricornis crispus*) war eine sichere Unterscheidung im brunftnahen Zeitraum sogar durch histologische Untersuchung nicht möglich (Kita et al. 1987). Der von uns ermittelte durchschnittliche Maximaldurchmesser der Corpora lutea liegt über jenem, der bei Gemsen (*Rupicapra rupicapra*) gemessen wurde (11 mm, Valentinčič et al. 1974; 11,5 mm, Salzmann 1977). Kita et al. (1987) fanden im Verlauf der Trächtigkeit eine Größenabnahme, Valentinčič et al. (1974) konnten keine Größenänderung feststellen.

Im Freiland findet die Brunft meist im Dezember bis Anfang Januar statt (Rauch 1937; Couturier 1962; Äschbacher 1978; Ratti 1986; Nievergelt und Zingg 1986). Unsere Daten bestätigen diese Angaben. Als späteste Konzeptionstermine werden 19. Februar (Couturier 1962) und 28. Februar (Stüwe und Grodinsky 1987) angegeben. Der Befund bei einer am 21. August 1989 erlegten, trächtigen 12jährigen Steingeiß der Kolonie Albris (die Frucht war ohne pathologische Veränderun-

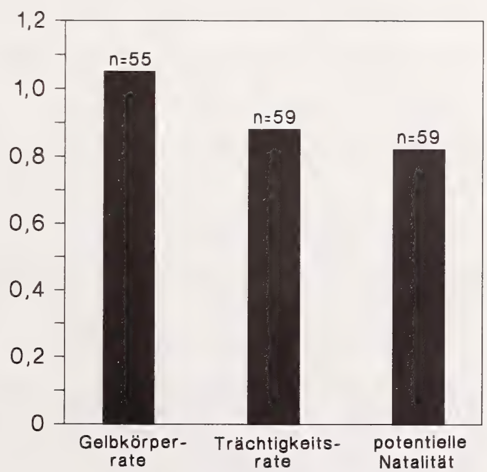

Abb. 3. Drei Fortpflanzungsraten bei den geschlechtsreifen Steingeißen der Kolonie Abris

gen) läßt vermuten, daß bei freilebenden Alpensteinböcken Konzeptionen in seltenen Fällen auch noch im Monat März möglich sind.

Steingeißen setzen in freier Wildbahn erstmals mit 3 bis 5 Jahren, in der Regel mit 4 Jahren (Ratti 1981). Diese Angaben werden durch unsere Untersuchungen bestätigt. In Gehegen gehaltene Steingeißen können hingegen bereits im zweiten Lebensjahr geschlechtsreif sein (Couturier 1962; Nievergelt 1966b; Stüwe und Grodinsky 1987). Die Ergebnisse von Nievergelt (1966a), wonach viele Geißen der Kolonie Albris erst im 6. Altersjahr zu setzen beginnen, können nicht bestätigt werden. Die Verzögerung des durchschnittlichen Eintrittes der Geschlechtsreife bei Erreichen der Lebensraumkapazität dürfte beim freilebenden Alpensteinbock nicht wesentlich mehr als 1 Jahr betragen.

Bei Rindern (*Bos primigenius* f. taurus) und den kleinen Hauswiederkäuern wird die Absterberate in der frühen Embryonalphase, der Periode der höchsten Gefährdung, mit 20 bis 50 % angegeben (Walser 1990). Bei Rehen (*Capreolus capreolus*) wurden Raten von 6,6 % (Borg 1970) und 3,2 % (Ellenberg 1978) angegeben. Die von uns gefundene Rate scheint, nachdem sie sich auf Postimplantationsverluste bezieht, relativ hoch zu sein, obwohl noch nicht von einem gehäuften Auftreten gesprochen werden kann.

Die Fekunditätsraten der 3- bis 13jährigen bzw. der 1- bis 15jährigen Geißen betragen im Wildpark Peter und Paul in St. Gallen 0,99 bzw. 0,78 (Stüwe und Grodinsky (1987), 25 % bzw. 24 % mehr als die entsprechenden für die Kolonie Albris gefundenen Raten. Die höhere Reproduktionsleistung in Wildgehegen kann insbesondere mit dem häufigeren Vorkommen von Zwillingsgeburten (Nievergelt 1966a) und mit dem früheren Eintritt der Geschlechtsreife erklärt werden.

Nievergelt (1966a) gibt für die Kolonie Albris eine Nachwuchsrate von 0,44 ± 0.17 an, Peracino und Bassano (1990) für die Steinbockpopulation des Parco Nazionale Gran Paradiso eine Natalität von 0,39–0,50. Beide Raten sind deutlich niedriger als die in dieser Arbeit gefundene potentielle Natalität. Die Anzahl der tatsächlich vorhandenen Kitze kann in typischen Steinbocklebensräumen in den Monaten Juni oder Juli nicht immer mit ausreichender Genauigkeit erfaßt werden (Rauch 1937). Zudem muß davon ausgegangen werden, daß auch in freier Wildbahn ein gewisser Anteil der gesetzten Kitze in den allerersten Wochen nach der Geburt eingeht. Dieser Anteil liegt bei verschiedenen Wildwiederkäuerarten zwischen 17 und 61 % (Kurt 1968; Staines 1970; Ellenberg 1978; Ballard et al. 1991; Whitten et al. 1992). Die reale Natalität dürfte beim freilebenden Alpensteinbock am besten durch die potentielle Natalität als höchstmögliche Zahl charakterisiert werden (vgl. Kirkpatrick 1980). Zur Vermeidung einer unkorrekten Interpretation von Angaben zur Fortpflanzungsleistung bei freilebenden Alpensteinbockpopulationen wird angeregt, die Begriffe Natalität und Nachwuchsrate ausschließlich bei Gebärmutteruntersuchungen in der Postimplantationsphase zu verwenden. Für die Bezeichnung der Anzahl der im Anschluß an die Setzperiode durch Direktbeobachtung gezählten Kitze bezogen auf die Gesamtzahl fortpflanzungsfähiger bzw. adulter Geißen sollte der Begriff Kitzrate verwendet werden, wobei stets der Beurteilungszeitpunkt und die bei den Geißen gewählte Altersklasse mitangegeben werden müßten.

In freier Wildbahn setzen Geißen jährlich 1 Kitz, sehr selten 2 (Couturier 1962; Ratti 1981), eine Aussage, die durch unsere Untersuchung bestätigt wird. Heptner et al. (1966) fanden beim sibirischen Steinbock (*Capra i. sibirica*) in einer Population in Zentraltienschan und im Pamir 2 Zwillingsträchtigkeiten unter 56. Daraus resultiert eine Rate von 3,6 %, die mit jener in dieser Arbeit gefundenen vergleichbar ist. In Wildgehegen kann die Häufigkeit von Zwillingsgeburten 29 % erreichen (vgl. Nievergelt 1966a). Wie im Wildpark Peter und Paul (Stüwe und Grodinsky 1987) war ein leichter Überhang der männlichen Kitze festzustellen. Allerdings ist die Größe der Stichprobe für eine schlüssige Aussage noch zu gering.

Danksagung

Ein besonderer Dank gilt den Wildhütern D. Godli, J. Schaniel und A. Plozza, dem Jagdaufseher E. Eggenberger und lic. phil. II H. Jenny für Organisation und Durchführung der Probenentnahme sowie für die Angaben über die Steinbockkolonie Albris. Bestens gedankt wird Dr. F. Tolari für die serologischen Untersuchungen, Dipl.-Ing. F. Völk und Dr. F. Reimoser für die konstruktiven Gespräche, Prof. Dr. K. Zerobin für die kritische Durchsicht des Manuskriptes sowie A. Körber für die Gestaltung der Abbildungen. Der Aufenthalt des Erstautors am Forschungsinstitut für Wildtierkunde und Ökologie der Veterinärmedizinischen Universität Wien wurde durch ein Stipendium des Schweizerischen Nationalfonds zur Förderung der wissenschaftlichen Forschung ermöglicht. Dem Leiter des Instituts, O. Univ. Prof. Dr. K. Onderscheka, wird für die breite Unterstützung bestens gedankt.

Zusammenfassung

Zur Beurteilung der Reproduktionsleistung des Alpensteinbockes (*Capra i. ibex* L.) wurden Uteri und Ovarien von 80 Geißen untersucht. Die Tiere stammten aus der Kolonie Albris (Graubünden, Schweiz) und wurden in den Monaten Dezember bis Juni der Jahre 1989–1990 und 1990–1991 erlegt.

Die Geißen konzipierten zwischen dem 1. Dezember und dem 21. Januar und wurden frühestens mit 2 Jahren geschlechtsreif. Die Konzeptionsrate der 2jährigen Geißen betrug 0,13, diejenige der 3jährigen 0,56, jene der 4jährigen Geißen 1. Die Trächtigkeitsrate lag bei 0,88. Bei 70 zweijährigen und älteren Geißen konnten 48 entwicklungsfähige Keimlinge nachgewiesen werden (Fekunditätsrate 0,69). Für die Altersklasse der 4- bis 13jährigen Geißen betrug die Fekunditätsrate 0,83. Mit 14 Jahren konnte ein wahrscheinlich altersbedingtes Nachlassen der Fortpflanzungsleistung festgestellt werden. Bei 59 geschlechtsreifen Geißen wurden 48 entwicklungsfähige Keimlinge gefunden, was eine potentielle Natalität von 0,81 ergibt. Die Fertilität betrug 0,25. Zwillingsträchtigkeiten wurden lediglich in einem unter 52 Fällen nachgewiesen (1,9 %).

Die in dieser Arbeit festgestellte Fortpflanzungsleistung übersteigt die bisher für diese Alpensteinbockpopulation angenommene deutlich.

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Anschriften der Verfasser: Dr. Marco Giacometti, Forschungsinstitut für Wildtierkunde und Ökologie der Veterinärmedizinischen Universität Wien, Savoyenstr. 1, A-1160 Wien; Dr. Peider Ratti, Jagd- und Fischereiinspektorat Graubünden, Loestr., CH-7000 Chur

Z. Säugetierkunde 59 (1994) 181–188

ISSN 0044-3468

Où se situe la limite nord de répartition géographique de *Myotis blythii* (Chiroptera: Vespertilionidae) en Europe centrale?

Par R. Arlettaz, A. Beck, R. Güttinger, Miriam Lutz, M. Ruedi et P. Zingg

Institut de Zoologie et d'Ecologie Animale, Université de Lausanne, Suisse et Ethologie und Wildforschung, Zoologisches Institut, Universität Zürich, Suisse

Réception du Ms. 15. 11. 1193
Acceptation du Ms. 05. 05. 1994

Abstract

Where is the northern border of the distribution range of Myotis blythii (Chiroptera: Vespertilionidae) in Middle Europe?

At least four mouse-eared bat colonies from the Swiss Rhine Valley visited in 1993 were mixed nursery roosts of *M. myotis* and *M. blythii* and not pure populations of *M. myotis* as previously believed. The recent discovery of *M. blythii* in that area does not result from a recent colonization process, but from the misidentification of these two cryptic species up to now. The northernmost mixed nursery found in Switzerland is located just a few dozen kilometers from Germany where *M. blythii* has apparently never been recorded. It is suggested to check the identity of further nursery roosts in Central Europe in order to avoid autoecological research on populations which may actually not be conspecific.

Introduction

Si le Grand Murin *Myotis myotis* est une espèce répandue sur l'ensemble du territoire helvétique, des dizaines de colonies étant connues dans le Moyen-Pays (Stutz et Haffner 1991), la répartition du Petit Murin *Myotis blythii* semblait jusqu'ici limitée au sud de la Suisse où l'espèce cohabite dans ses gîtes avec le Grand Murin (Moretti et al. 1993). Seules quatre colonies abritant *M. blythii* étaient jusqu'ici connues en Suisse, trois en Valais (Alpes centrales du sud-ouest de la Suisse) et une au Tessin (versant sud des Alpes). Par ailleurs, une seule mention existait à cette date en Suisse en dehors du Tessin et du Valais: un individu mâle collecté par Bovey (1954) dans les souterrains du château de Chillon/ Montreux (Musée zoologique Lausanne No 1556), et attribué à *M. myotis* est en fait un *M. blythii* (Ruedi 1987; Moretti et al. 1993). En septembre 1993, dans le cadre des études de sa thèse de doctorat, R. Arlettaz visitait les colonies de Murins connues dans les Grisons, en vue d'effectuer des mensurations de la morphologie externe d'une population allopatrique de Grand Murin *M. myotis*. A notre plus grande surprise, il s'est avéré que les quatre gîtes visités abritaient tous une importante proportion de *M. blythii* intimement associés aux *M. myotis*. Ces faits nous ont incités à visiter d'autres colonies, notamment dans le nord-est de la Suisse, afin de préciser la répartition géographique du Petit Murin en Suisse.

Matériel et méthodes

Colonies examinées

Selon les travaux de Lutz (1986 et comm. pers.), cinq colonies de reproduction de Grand Murin existent dans les Grisons; elles sont toutes quatre situées dans la vallée du Rhin, soit de l'amont vers l'aval: à Surrein, à Trun (colonie très proche de la précédente, habitée probablement par les mêmes individus) et Laax (Surselva), à Pratval dans le Domleschg, enfin à Fläsch aux confins du Liechtenstein et du Vorarlberg autrichien. Les trois colonies de reproduction les plus accessibles (la colonie de Pratval ne permet pas de capture directe des animaux) ainsi qu'un gîte occupé soit par des mâles

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solitaires soit par des couples durant la période d'accouplement ont été vistés les 9 et 10 septembre 1993. Les 15 et 16 septembre, nous avons visité l'église d'Eichberg, qui est la colonie la plus nordique connue dans la vallée du Rhin helvétique, ainsi que les colonies d'Oberglatt/Flawil (en bordure du Plateau et des préalpes saint-galloises et appenzelloises), de Lipperswil (Plateau thurgovien à proximité du lac de Constance) et de Veltheim (pied sud du Jura argovien). Nous disposons par ailleurs d'informations récentes au sujet de la colonie de Meiringen, Oberland bernois (visitée en 1992) ainsi que sur celles d'Eysins, dans le bassin lémanique, au pied du Jura vaudois (1992) et de Roche (vallée vaudoise du Rhône, visitée en 1991).

Identification

L'identification des espèces a été établie sur la base des critères de la morphologie extérieure proposés par Arlettaz et al. (1991): 1. précence d'une tache blanche sur la tête des Petits Murins qui permet d'effectuer un premier repérage visuel dans les essaims; 2. mesure de la longueur de l'avant-bras et de celle de l'oreille, qui permettent, lorsqu'on les associe dans une fonction discriminante, de séparer correctement les deux espèces. Au total, nous avons capturé et mesuré 102 individus différents (Tableau). Ce lot ne représente pas un échantillonnage aléatoire, l'accent ayant été mis sur la capture des Petits Murins en priorité, du moins là où ils existaient (29 *M. blythii* vs. 73 *M. myotis* au total). La visite des colonies a eu lieu après une période fraîche et maussade, et la dislocation postreproductrice était déjà bien entamée, preuve en est le nombre de jeunes de l'année capturés au sein des colonies de parturition (71.6 %, soit 68 immatures sur 95 individus d'âge connu, gîte d'accouplement non compris). Il faut par ailleurs savoir que la mise-bas est plus tardive chez *M. blythii*, ce qui a pour corollaire une dispersion plus tardive des femelles adultes et des immatures chez cette espèce, en tout cas en Suisse (Arlettaz, inédit). En conséquence, il est probable que les estimations des proportions des deux espèces au sein des colonies mixtes (cf. ci-dessous) sont biaisées en faveur des Petits Murins.

Résultats

La colonie de Surrein comportait un essaim principal totalisant environ 250 chauves-souris dont 20 à 30 % étaient de la petite espèce. L'église de Laax comptait 100 à 150 individus dont un quart à un tiers de *M. blythii*. Le gîte d'accouplement de Bonaduz totalisait 7 couples ainsi que deux individus isolés; deux des couples appartenaient à la petite espèce *M. blythii*, alors que cinq étaient des couples de *M. myotis*. L'église de Fläsch qui rassemble plus de 1200 têtes en période d'élevage ne contenait plus qu'environ 140 individus dispersés en quatre essaims distincts lors de notre visite. Trois essaims étaient composés en majorité (plus de 95 % des individus) de *M. myotis* tandis que le quatrième essaim ne contenait pratiquement que la Petite espèce (soit une total estimé à 100 *M. myotis* et 40 *M. blythii*). Les Murins de l'église de Eichberg (50–100 animaux lors de notre visite) ne pendent pas librement dans la sous-pente, mais gîtent dans l'entretoit, ce qui a rendu impossible l'estimation des proportions des deux espèces. Les chauves-souris de Oberglatt/Flawil (environ 50 individus lors de notre visite) se retirent également dans les fissures entre charpente et couverture du clocher ou des combles; 32 individus capturés étaient tous des *M. myotis*. A Lipperswil, où il restait encore 50–60 individus, et à Veltheim (1400 individus en période de reproduction, soit la plus grande colonie de Murins connue en Suisse; 150 individus lors de la visite), les chauves-souris pendaient librement sous les lambris. Ces deux dernières colonies n'abritaient aucun *M. blythii*. Enfin, les colonies de Meiringen et d'Eysins sont également à considérer comme des colonies pures de Grand Murin. La carte (Fig.) présente la localisation des colonies mixtes et pures visitées dans le cadre de cette étude.

Discussion

La difficulté d'identifier ces deux espèces jumelles de Murins sur la base de leur morphologie externe explique que la présence de colonies mixtes ait passé inaperçue dans le nord-est de la Suisse. A cet égard, il faut rappeler que ce n'est que récemment que la distinction génétique entre *M. myotis* et *M. blythii* a été établie (Ruedi et al. 1990) et que c'est par le

Localité, sexe âge, longueur de l'avant-bras, longueur de l'oreille, score discriminant (*M. myotis*: z > 0; *M. blythii*: z < 0) et appartenance spécifique des Murins capturés dans les colonies du nord-est de la Suisse dans le cadre de la présente étude

La méthode d'identification au moyen des scores discriminants est décrite par ARLETTAZ et al. (1991)

Localité	Sexe	Âge	Avant-bras (mm)	Longueur oreille (mm)	Score discriminant (z)	Espèce
Surrein GR	w	ad	61.0	22.7	–1.821	*M. blythii*
	w	subad	60.9	26.7	3.835	*M. myotis*
	m	subad	52.7	22.8	–2.579	*M. blythii*
	m	?	54.7	22.4	–2.929	*M. blythii*
	w	ad	61.1	26.5	3.573	*M. myotis*
	m	subad	52.8	22.3	–3.277	*M. blythii*
	w	subad	58.0	23.5	–1.013	*M. blythii*
	w	subad	60.0	23.8	–0.371	*M. blythii*
	m	?	58.9	23.8	–0.490	*M. blythii*
	m	ad	54.0	23.0	–2.155	*M. blythii*
	w	ad	57.5	23.5	–1.067	*M. blythii*
	m	ad	59.7	25.6	2.146	*M. myotis*
	w	ad	61.4	25.7	2.472	*M. myotis*
	w	ad	62.0	25.6	2.396	*M. myotis*
	w	subad	60.8	26.4	3.399	*M. myotis*
Laax GR	m	subad	53.0	21.6	–4.247	*M. blythii*
	m	subad	58.1	25.6	1.973	*M. myotis*
	w	subad	59.8	23.8	–0.393	*M. blythii*
	w	subad	59.3	24.3	0.261	*M. blythii*
Bonaduz GR	m	ad	60.1	25.6	2.190	*M. myotis*
	m	ad	60.9	25.1	1.568	*M. myotis*
	w	ad	59.5	26.2	2.974	*M. myotis*
	w	ad	54.8	23.3	–1.643	*M. blythii*
	w	ad	61.4	26.6	3.747	*M. myotis*
	m	ad	57.0	25.5	1.712	*M. myotis*
	m	ad	60.0	25.5	2.037	*M. myotis*
Fläsch GR	m	subad	53.2	23.8	–1.108	*M. blythii*
	m	ad	53.3	24.0	–0.814	*M. blythii*
	w	subad	58.3	22.9	–1.830	*M. blythii*
	w	subad	56.0	23.1	–1.796	*M. blythii*
	m	subad	57.0	22.8	–2.113	*M. blythii*
	w	subad	57.6	23.5	–1.056	*M. blythii*
	m	subad	57.0	23.2	–1.546	*M. blythii*
	m	subad	55.1	22.5	–2.744	*M. blythii*
	m	subad	55.2	24.4	–0.042	*M. blythii*
	m	subad	57.0	23.1	–1.688	*M. blythii*
Oberglatt SG	w	subad	59.3	26.1	2.811	*M. myotis*
	m	subad	57.1	26.2	2.714	*M. myotis*
	w	subad	60.7	26.1	2.963	*M. myotis*
	m	subad	60.9	27.3	4.684	*M. myotis*
	w	subad	57.9	26.0	2.518	*M. myotis*
	m	ad	58.1	27.4	4.523	*M. myotis*
	w	subad	59.0	26.5	3.345	*M. myotis*
	w	subad	59.3	26.4	3.236	*M. myotis*
	m	subad	59.7	26.5	3.421	*M. myotis*
	w	subad	55.9	26.8	3.434	*M. myotis*
	w	subad	59.4	26.8	3.814	*M. myotis*
	w	subad	61.0	27.9	5.545	*M. myotis*
	w	subad	59.2	26.5	3.367	*M. myotis*
	w	subad	62.5	25.5	2.308	*M. myotis*
	w	ad	60.7	26.4	3.388	*M. myotis*
	w	subad	61.1	26.0	2.865	*M. myotis*
	w	ad	63.5	27.9	5.816	*M. myotis*

Tableau (suite)

Localité	Sexe	Âge	Avant-bras (mm)	Longueur oreille (mm)	Score discriminant (z)	Espèce
Oberglatt SG	w	subad	58.0	26.9	3.803	*M. myotis*
	m	subad	55.2	25.8	1.942	*M. myotis*
	m	subad	58.6	26.2	2.877	*M. myotis*
	m	subad	55.9	25.3	1.309	*M. myotis*
	m	subad	58.2	25.6	1.984	*M. myotis*
	w	subad	60.7	27.2	4.521	*M. myotis*
	w	subad	61.0	26.8	3.987	*M. myotis*
	w	subad	59.1	26.6	3.498	*M. myotis*
	w	subad	58.0	25.8	2.245	*M. myotis*
	w	subad	59.3	27.0	4.086	*M. myotis*
	w	subad	61.5	27.0	4.325	*M. myotis*
	m	subad	56.6	25.7	1.952	*M. myotis*
	m	subad	61.5	26.4	3.475	*M. myotis*
	m	subad	60.3	25.6	2.211	*M. myotis*
	m	subad	58.3	25.5	1.853	*M. myotis*
Eichberg SG	m	subad	55.2	22.7	–2.450	*M. blythii*
	m	subad	55.0	22.6	–2.613	*M. blythii*
	w	subad	58.3	22.6	–2.255	*M. blythii*
	m	subad	57.0	24.8	0.720	*M. myotis*
	w	subad	57.3	23.7	–0.806	*M. blythii*
	w	subad	58.3	22.5	–2.397	*M. blythii*
	m	subad	57.9	25.6	1.951	*M. myotis*
	m	subad	54.7	23.7	–1.087	*M. blythii*
	w	subad	57.7	26.7	3.488	*M. myotis*
	w	subad	64.3	25.8	2.928	*M. myotis*
	w	ad	63.0	25.4	2.221	*M. myotis*
	m	subad	58.7	26.1	2.746	*M. myotis*
Lipperswil TG	w	subad	61.0	26.0	2.854	*M. myotis*
	w	subad	58.4	26.2	2.855	*M. myotis*
	m	subad	58.0	25.2	1.395	*M. myotis*
	w	subad	60.5	25.4	1.950	*M. myotis*
	w	subad	59.8	25.5	2.015	*M. myotis*
	w	subad	57.4	26.2	2.747	*M. myotis*
	w	subad	57.0	24.7	0.579	*M. myotis*
	w	subad	60.0	25.8	2.462	*M. myotis*
Veltheim AG	m	subad	56.9	26.1	2.551	*M. myotis*
	w	ad	62.4	26.4	3.572	*M. myotis*
	w	subad	61.4	25.4	2.047	*M. myotis*
	w	subad	60.1	25.6	2.190	*M. myotis*
	m	subad	58.7	26.1	2.746	*M. myotis*
	w	subad	60.3	26.8	3.911	*M. myotis*
	w	subad	61.0	25.5	2.145	*M. myotis*
Meiringen BE	w	subad	63.1	26.4	3.648	*M. myotis*
	w	ad	58.7	25.7	2.179	*M. myotis*
	w	ad	60.9	26.3	3.268	*M. myotis*
	w	ad	64.2	26.3	3.626	*M. myotis*
	w	ad	63.5	26.0	3.125	*M. myotis*
	w	ad	62.0	25.0	1.546	*M. myotis*
	w	ad	59.0	24.5	0.512	*M. myotis*

AG = Argovie ; BE = Berne; GR = Grisons; SG = St-Gall; TG = Thurgovie, soit les différents cantons suisses où se trouvent les colonies de parturition (les sites sans reproduction n'ont pas été cartographiés) étudiées dans le cadre de la présente étude.

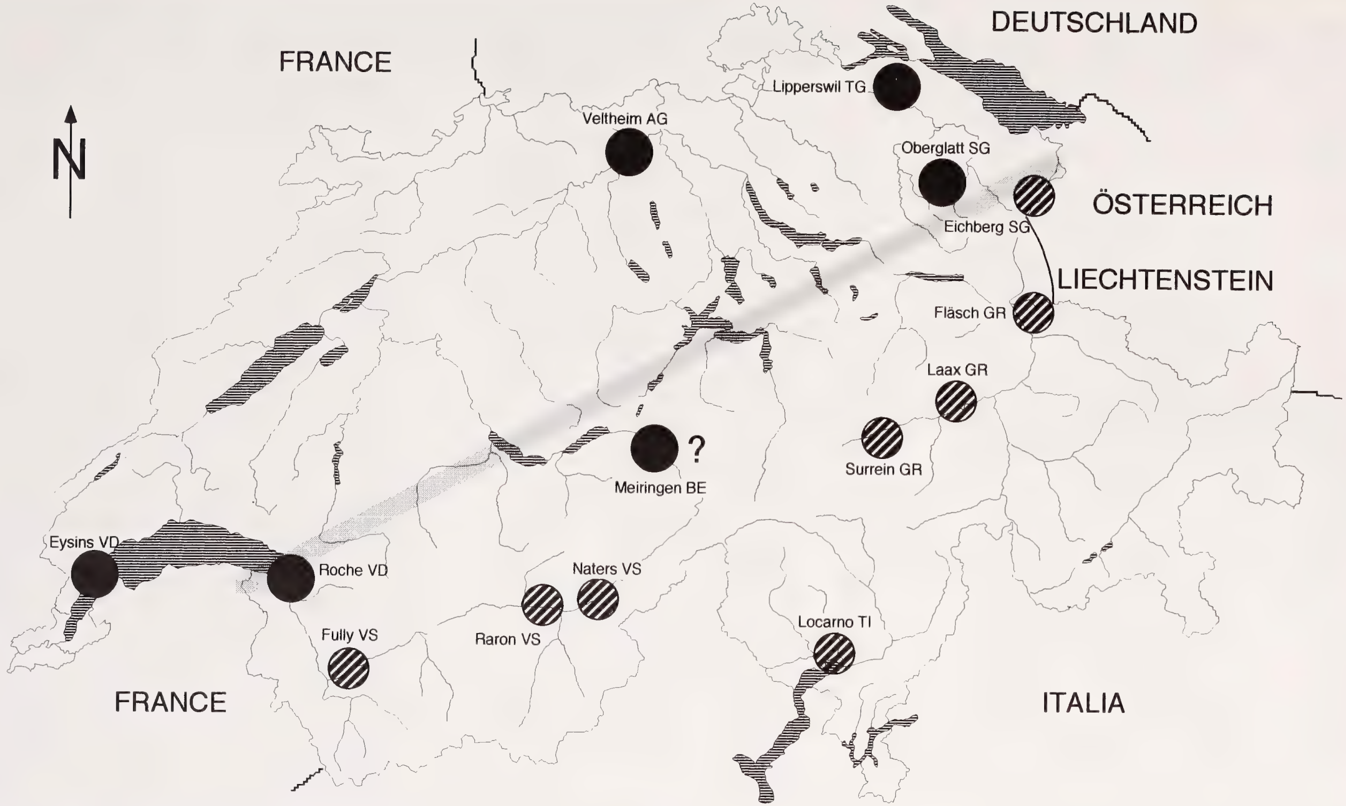

Fig. 1. Répartition géographique et localités des colonies pures de *M. myotis* (noir) et mixtes de *M. myotis* et *M. blythii* (strié) récemment recensées en Suisse. La bande grisée indique le front nord du massif alpin qui semble correspondre à la limite de distribution de *M. blythii* en Suisse. Le point d'interrogation indique une colonie supposée pure de *M. myotis* qui mériterait toutefois confirmation. Les initiales indiquent les différents cantons suisses où se trouvent les colonies: TI = Tessin; VD = Vaud, VS = Valais; pour les autres initiales, voir légende du tableau

biais de cette approche que Arlettaz et al. (1991) ont été en mesure de mettre au point une méthode de détermination sur le terrain plus rigoureuse que ce ne fut le cas précédemment. Notons toutefois que la simple récolte et mensuration des crânes des cadavres d'adultes ou subadultes qui finissent fatalement par se retrouver sous les essaims auraient permis de déceler la présence de la petite espèce, les différences crâniennes interspécifiques étant décrites de longue date en Europe centrale (e.g. Strelkov 1972). En Suisse orientale, l'accent particulier qui a été mis sur la protection de ces colonies, et qui s'accompagnait d'une quasi absence de capture, a reporté la découverte de ces deux espèces cryptiques à une date bien tardive. Sur la soixantaine de colonies recensées en Suisse orientale et attribuées par Stutz et Haffner (1991) à la seule espèce *M. myotis*, quatre au moins se sont avérées des colonies mixtes lors de nos visites. Et il est probable que trois autres colonies au moins (Pratval/Grisons, Triesen/Liechtenstein, Gams/St-Gall) sont aussi habitées par *M. blythii*, puisque situées entre et à peu de distance des colonies mixtes précitées. Une proportion non négligeable des colonies de Murins recensées en Suisse orientale seraient donc des colonies mixtes. On notera également que toutes les colonies mixtes aujourd'hui connues en Suisse sont situées dans le massif alpin. Dans ce contexte, on peut s'interroger sur le statut exact des colonies de Suisse centrale, notamment celles existant dans les vallées soumises à un régime de foehn; à cet égard, un nouveau contrôle de la colonie de Meiringen se justifierait, seuls 7 individus y ayant été capturés en 1992 (Tableau). Enfin, qu'en est-il des régions limitrophes (Bavière du sud) situées à quelques dizaines de kilomètres seulement de la colonie mixte la plus nordique de Suisse? D'autant plus que Spitzenberger (1988) mentionne la présence d'une colonie de *M. blythii* dans la vallée de l'Inn (Tyrol autrichien), à une latitude comparable à la colonie helvétique mixte la plus nordique. Le bassin de Rosenheim, situé dans le prolongement naturel de la vallée de l'Inn et aux portes des Alpes est-il vraiment habité par la seule espèce *M. myotis*? Les études intensives effectuées au cours de la dernière décennie dans cette région concernent-elles vraiment des colonies pures de Grand Murin? Il est urgent que les chiroptérologistes d'Europe centrale, notamment de France septentrionale, de Suisse et d'Allemagne, effectuent un nouveau contrôle de leurs colonies afin qu'une réponse définitive soit apportée à cette question cruciale. Sinon, on peut redouter que certains travaux de recherche soient à considérer, au moins partiellement, comme caducs, à l'exemple des études de Ackermann (1984) et de Graf et al. (1992) qui portaient sur la biologie et le régime alimentaire de *M. myotis* en Suisse orientale. Ces deux chercheurs on étudié sans le savoir des colonies mixtes et non des colonies pures de Grand Murin. Une immigration récente de *M. blythii* dans cette région est à écarter, les habitats de chasse (milieux herbacés; voir Arlettaz et al. 1993) dont l'espèce dépend ayant plutôt subi une diminution ou une péjoration (engraissement) qu'une extension au cours des dernières années. Ackermann (1984) qui a justement travaillé à Eichberg, dans la vallée du Rhin, décrit le régime alimentaire, les routes de vol, les rythmes d'activité, et accessoirement les zones de chasse de sa colonie supposée pure. Or, il est fort probable que ses observations concernent les deux espèces. Parmi les 14 gîtes étudiés par Graf et al. (1992) dans le cadre d'une comparaison géographique du régime alimentaire de *M. myotis* en Suisse orientale, trois au moins se sont avérées des colonies mixtes. Ainsi, la proportion inférieure des Carabidae et la part supérieure des Acrididae en région alpine, pour ne citer que ces deux groupes particulièrement évidents, n'a vraisemblablement pas pour origine principale la différence dans l'offre du milieu mais dans le fait que l'on a étudié deux expèces aux régimes alimentaires bien tranchés (Arlettaz et al. 1993) au lieu d'une seule. En effet, Arlettaz et al. (1993) ont récemment montré que, dans les Alpes valaisannes (sud-ouest de la Suisse), *M. myotis* capture surtout des Carabes tandis que *M. blythii* préfère les Orthoptères appartenant à la famille Tettigoniidae. D'autres travaux en cours sur l'écologie de ces deux espèces en conditions de sympatrie et d'allopatrie, devraient permettre de mieux cerner les exigences de *M. blythii* du point de vue habitat et régime alimentaire, et partant d'expliquer sa distribution géographique en Europe.

Remerciements

Nous remercions les responsables des édifices publics et sacrés qui nous ont permis d'accéder aux différentes colonies visitées, en particulier M. W. D. Burkhard.

Résumé

Une visite effectuée en 1993 dans les colonies de Vespertilions murins de la vallée helvétique du Rhin (cantons des Grisons et de Saint-Gall) ont montré que quatre nurseries au moins y abritaient les deux espèces jumelles *M. myotis* et *M. blythii* et non des populations pures de *M. myotis* comme on le pensait jusqu'alors. Ceci porte à huit le total des nurseries mixtes qui ont été localisées à ce jour en Suisse. La découverte récente du Petit Murin dans les cantons des Grisons et de Saint-Gall ne résulte pas d'une colonisation récente, mais d'une non reconnaissance de cette espèce cryptique. La colonie suisse la plus nordique est située au sud du lac de Constance (Bodensee) et à quelques dizaines de kilomètres seulement de la Bavière (Allemagne) où l'espèce n'a jamais été signalée. Les auteurs insistent sur la nécessité de procéder à une nouvelle identification des Murins des colonies connues en Europe centrale, notamment dans la moitié nord de la France, le sud de l'Allemagne et l'Autriche, afin de mieux cerner l'aire de répartition géographique du Petit Murin et d'éviter des études autoécologiques sur des populations qui seraient en réalité mixtes.

Zusammenfassung

Wo liegt die nördliche Verbreitungsgrenze von Myotis blythii (Chiroptera: Vespertilionidae) in Mitteleuropa?

Eine 1993 erfolgte Kontrolle von Wochenstuben-Quartieren im schweizerischen Rheintal (Kantone Graubünden und St. Gallen) hat ergeben, daß mindestens vier der bisher in der Region gefundenen Mausohr-Wochenstuben sowohl *Myotis myotis* wie *Myotis blythii* beherbergen. Bis zum heutigen Tag sind damit insgesamt acht Mischkolonien der beiden Arten in der Schweiz nachgewiesen. Mischkolonien waren bisher nur aus dem Wallis (3) und dem Tessin (1) bekannt. Die erst jetzt bekannt gewordenen Vorkommen von *M. blythii* weisen auf ein bisheriges Übersehen dieser Fledermausart hin und weniger auf eine erst kürzlich erfolgte Besiedlung neuer Gebiete. Die nördlichste Kolonie mit *M. blythii* in der Schweiz liegt wenige Kilometer südlich des Bodensees und damit nur wenige Dutzend Kilometer entfernt von Bayern (Deutschland), wo die Art bisher nicht nachgewiesen ist. Aufgrund der vorliegenden Befunde erachten es die Autoren der vorliegenden Arbeit als dringend nötig, sämtliche Mausohrkolonien in Mitteleuropa von neuem auf ihre Artzugehörigkeit zu überprüfen, vor allem in der nördlichen Hälfte Frankreichs sowie in Süd-Deutschland und Österreich. Dadurch könnte die geographische Verbreitung von *M. blythii* präziser erfaßt und somit künftig verhindert werden, daß autökologische Untersuchungen irrtümlicherweise an Kolonien durchgeführt werden, welche tatsächlich gemischte Kolonien von *M. myotis* und *M. blythii* sind.

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Adresses des auteurs: Raphaël Arlettaz, Institut de Zoologie et d'Ecologie Animale, Bâtiment de Biologie, Université de Lausanne, CH-1015 Lausanne; Andres Beck, Zweiern 19, CH-5443 Niederrhordorf; René Güttinger, Ethologie und Wildforschung, Zoologisches Institut, Universität Zürich, Irchel 2, CH-8057 Zürich; Miriam Lutz, Encarden 51, CH-7152 Sagogn; Dr. Manuel Ruedi, Institut de Zoologie et d'Ecologie Animale, Bâtiment de Biologie, Université de Lausanne, CH-1015 Lausanne; Dr. Peter Zingg, Riedmattenweg 19, CH-3700 Spiezwiler, Suisse

Z. Säugetierkunde 59 (1994) 189–191

ISSN 0044-3468

WISSENSCHAFTLICHE KURZMITTEILUNG

Feeding habits of the Stone marten *Martes foina* and environmental factors in western France

By Th. Lode

Laboratoire d'Ethologie, Université Rennes 1, Rennes, France

Receipt of Ms. 8. 9. 1993
Acceptance of Ms. 12. 1. 1994

The stone marten *Martes foina* Erxleben, 1777 has been portrayed as an omnivorous feeder (Waechter 1975; Delibes 1978; Amores 1980; Chotolchu et al. 1980; Clement and Saint-Girons 1982; Holisova and Orbtel 1982; Kalpers 1983; Rasmussen and Madsen 1985; Skirnisson 1986; Tester 1986; Romanowski and Lesinski 1991); moreover, it has been assumed that food availabilities affect diet composition. Although some previous studies have assessed seasonal dietary patterns, only very few have attempted to evaluate in parallel resource availabilities (Lode 1991). The aim of the present investigation is to relate abiotic factors and the main resource availabilities to a detailed study of the diet of stone martens.

The study was performed in farmlands in the Brière regional Parc (47° 26′ N, 2° 14′ W) and near marshes of the Lake Grand-Lieu (47°01′ N, 1°46′ W). The climate is mild and humid, mean temperatures ranging between 21.5 °C in August (1990) (Grand-Lieu) and 2.9 °C in February (1991) (Brière), precipitation reached 851 mm per year over 140 to 153 rainy days.

In Brière, 663 scats from stone martens were collected monthly from February 1990 to November 1991, and 486 scats from July 1989 to December 1990 in Grand-Lieu, in barns used as resting places. Remains were assigned to the most specific taxon possible by examining the external characteristics and by microscopic observation of medullary hair structure and cross-section, compared with our collection and an atlas (Day 1966; Chaline et al. 1974; Debrot et al. 1982). Diet composition was estimated as frequency of occurrences. The trophic niche breadth was calculated using the Shannon index $h' = -\Sigma P_i \log_2 P_i$ where P_i was the frequency of a food category (mammals, birds, insects, fruit and other). Availability of *Microtus arvalis* was made by trapline success every second month. At each site, a line of 32 live-traps was set for 3 nights through two meadows. The relative abundance of rodents was expressed as the number of individuals captured per trapnight. The abundance of insects (mainly Orthoptera and Coleoptera) was ascertained by counting the number of individuals captured monthly in visual traps (Leberre 1969) in 3 habitats (wood, hedge, meadow). The fruit availability was estimated by ascribing a monthly rank order according to the ripeness and productivity of fruit in 3 control trees each for blackberry bush (*Rubus* sp.), sloe (*Prunus spinosa*), elder (*Sambucus nigra*) and apple tree (*Malus sylvestris*).

Dietary variations showed a clear seasonality (Brière, $\chi^2 = 159.4$, df 9, $p < 0.001$; Grand-Lieu $\chi^2 = 160.3$, df 9, $p < 0.001$). Mammals formed the bulk of the diet reaching 75 % of the winter diet in Brière and 84 % in Grand-Lieu but represented only 40 % and 31 % of the summer diet (Tab. 1). Birds were mainly consumed in spring and insects were especially found in summer. Fruit was of major importance during summer and autumn.

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Table 1. **Seasonal proportions of different food categories in Stone marten diet at two sites in western France**

	Brière				Grand-Lieu			
	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
Insectivores	5.4	0.0	0.0	4.6	4.7	0.0	1.4	4.9
Microtus	32.8	29.8	50.3	52.6	26.4	22.2	36.4	46.1
Other mammals	19.8	10.1	3.5	17.9	32.1	8.4	17.5	32.7
Total mammals	58.0	39.9	53.8	75.1	63.2	30.6	55.3	83.7
Birds	24.6	13.9	4.5	15.6	21.7	5.6	2.8	7.1
Insects	7.2	18.7	5.2	1.2	5.7	28.3	11.9	0.0
Fruit	7.8	25.9	35.8	6.3	7.5	33.9	25.8	4.2
Others	2.4	1.4	0.7	1.7	1.2	1.7	4.1	4.9
n prey =	*167*	*208*	*288*	*173*	*106*	*180*	*217*	*141*
h′ =	1.630	1.952	1.463	1.157	1.480	1.924	1.684	0.882

The niche breadth varied throughout the year with a minimum in winter and a maximum in summer. Annual diet was significantly different between the two sites ($\chi^2 = 24.22$, df 4, $p < 0.001$). In summer, birds represented a less important food category in Grand-Lieu than in Brière, while the proportion of insects and fruit was larger in Grand-Lieu ($\chi^2 = 14.9$, df 3, $p < 0.002$). During autumn, more insects and less fruit were eaten in Grand-Lieu than in Brière ($\chi^2 = 11.86$, df 3, $p < 0.008$). Due to the predominance of mammal prey, no significant difference appeared either in winter ($\chi^2 = 7.7$, $p > 0.05$) or in spring ($\chi^2 = 0.74$, $p > 0.8$).

Photoperiod and mean temperatures were negatively correlated with the monthly frequency of mammals in the diet (Spearman rank correlation, df 20 in Brière, df 16 in Grand-Lieu, Brière $r_s = -0.699$, $p < 0.001$ and $r_s = -0.845$, $p < 0.001$, Grand-Lieu $r_s = -0.798$, $p < 0.001$ and $r_s = -0.909$, $p < 0.001$), whereas the number of rainy days ($r_s = 0.448$, $p < 0.05$) in Brière and the number of rainy days and precipitations in Grand-Lieu were positively related ($r_s = 0.579$, $p < 0.02$, $r_s = 0.501$, $p < 0.05$). Close negative relationships were obtained between monthly frequency of *Microtus arvalis* and mean temperatures (Brière $r_s = -0.709$, $p < 0.001$, Grand-Lieu $r_s = -0.862$, $p < 0.001$) or photoperiod (Brière $r_s = 0.750$, $p < 0.001$, Grand-Lieu $r_s = -0.876$, $p < 0.001$). On the other hand, precipitation and number of rainy days were positively correlated with dietary frequency of voles (Brière $r_s = 0.494$, $r_s = 0.451$, $p < 0.05$, Grand-Lieu $r_s = 0.634$, $r_s = 0.605$, $p < 0.01$). A few insectivores were consumed during the coldest months. Other mammals eaten included long-tailed field mice (*Apodemus sylvaticus*), mice (*Mus domesticus*), brown rats (*Rattus norvegicus*), bank voles (*Clethrionomys glareolus*), water voles (*Arvicola sapidus*) and rabbits (*Oryctolagus cuniculus*). Birds were mainly passeriforms. Coleoptera and orthoptera were the most common insects found and showed correlations with photoperiod and temperatures (Brière $r_s = 0.874$, $r_s = 0.851$, $p < 0.001$, Grand-Lieu $r_s = 0.815$, $r_s = 0.934$, $p < 0.001$). Other invertebrates, mainly earthworms, were eaten in winter and spring. The frequency of fruit (*Rubus* sp., *Prunus* sp., *Sambucus niger, Malus sylvestris, Crataegus oxyacantha, Rosa canina*) correlated with temperatures (Brière $r_s = 0.544$, $p < 0.02$, Grand-Lieu $r_s = 0.806$, $p < 0.001$) and in Grand-Lieu to photoperiod ($r_s = 0.815$, $p < 0.001$), precipitations ($r_s = 0.575$, $p < 0.02$) and rainy days ($r_s = -0.623$, $p < 0.01$).

Availability of *Microtus arvalis* increased from spring to autumn (Tab. 2) but monthly variation of the trap-night index did not correlate with vole occurrence in the marten diet. Insect abundance showed an increase in summer, significantly correlated with occurrence of this category (Brière $r_s = 0.777$, $p < 0.005$ df = 12, Grand-Lieu $r_s = 0.947$, $p < 0.001$ df = 16). Fruit availability was greatest from July to October, associated with the fruit frequency in the diet (Brière $r_s = 0.894$, Grand-Lieu $r_s = 0.848$, $p < 0.001$).

Table 2. **Mean seasonal variations in availability index of three main food resources at two sites in western France**

	Brière				Grand-Lieu			
	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
Microtus	5.2	31.2	52.0	41.6	10.4	33.9	52.1	26.0
Fruit	0.0	16.3	25.6	0.0	0.0	19.2	31.8	0.0
Insects	11.7	67.0	36.0	0.0	7.3	67.2	36.7	0.0

Characteristics of feeding habits of *Martes foina* in western France particularly illustrated the trophic opportunism of this species. The diet showed a strong seasonality with a winter/spring diet based on *Microtus* alternating with a summer/autumn exploitation of insects and fruit. Not surprisingly, the diversity index reached its lowest level in winter and increased in summer, according to the increase of food availabilities. Close relationships found between abiotic variables, food availabilities and dietary variations emphasized the decisive influence of environmental factors on feeding ecology of the stone marten.

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Author's address: Dr. Thierry Lode, Laboratoire d'éthologie, Université de Rennes I, F-35042 Rennes, France

Tagung der Tierschutzkommission der DGS am Institut für Haustierkunde der Christian-Albrechts-Universität in Kiel

Am 24. April 1994 fand in Kiel das erste Treffen der neugegründeten Tierschutzkommission statt. Wichtiger Top dieser Sitzung war die Erarbeitung des Entwurfs einer Evaluierung der Eingriffe an Tieren in bezug auf ihren Schweregrad. Dieser Entwurf soll insbesondere für diejenigen DGS-Mitglieder eine Hilfestellung sein, die im Rahmen ihrer Feldforschung etwa Wildtiere fangen müssen (zum Zwecke der Markierung etc.).

Ein Konzept in Form eines Merkblattes soll unter Berücksichtigung des momentanen Standes der Tierschutzgesetzgebung Richtlinien bezüglich der Einordnung verschiedener Forschungsvorhaben geben (anmeldepflichtiger, genehmigungspflichtiger Tierversuch bzw. kein Tierversuch) und auf der Mitgliederversammlung in Wien 1994 zur Diskussion gestellt werden.

Tierschutzkommission der DGS:

Dr. Dorit Feddersen-Petersen, Institut für Haustierkunde, Christian-Albrechts-Universität, Olshausenstr. 40, D-24118 Kiel, Tel. (04 31) 8 80-45 06, Fax (04 31) 8 80-13 89 (Vorsitz).

Prof. Dr. Christian Welker, Gesamthochschule Kassel, Zoologie und vergl. Anatomie, Heinrich-Plett-Str. 40, D-34132 Kassel, Tel. (05 61) 8 04 46 04.

Dr. Andreas Haemisch, Medizinische Hochschule Hannover, Zentrales Tierlabor, D-30623 Hannover, Tel. (05 11) 5 32 37 47, Fax (05 11) 5 32 37 10.

Dr. Dieter Zscheile, Waldschulenweg 1, D-19061 Schwerin, Tel. (03 85) 21 33 01, Fax (03 85) 21 33 00.

Tagungsankündigungen

1. Fifth International Conference "Rodents and Spatium", Biodiversity and Adaptation. 20.–24. März 1995 in Rabat, Marokko, Institut Agronomique et Veterinaire Hassan II. Auskünfte: Dr. Abelkader Zaime, Convenor, Conference Rodents and Space, Departement de Physiologie Animale et Therapeutique, I.A.V. Hassan II, B.P. 6445 Rabat-Instituts, MA-10101 Rabat, Morocco. Fax (2 12-7) 77 71 19 oder 77 58 38.
2. VIII Curso Intensivo: 17. Oktober–22. Dezember 1994: Master Internacional en enfermedades Parasitarias Tropicales.
   Programas Erasmus y Comett de la UE
   Auskünfte: Universitat de Valencia, Departamento de Parasitologia, Fakultad de Farmacia. Av. Vicent Andres Estelles s/n, E-46100 Burjassot, Valencia, Espana, UE. Fax 34 63 86 47 69.

Erscheinungsweise und Bezugspreis 1994: 6 Hefte bilden einen Band. Jahresabonnement Inland: DM 378,– zuzüglich DM 13,80 Versandkosten; Jahresabonnement Österreich: öS 2949,– zuzüglich öS 164,– Versandkosten; Jahresabonnement Schweiz: sfr 364,– zuzüglich sfr 21,– Versandkosten; Jahresabonnement EG-Binnenmarkt-Länder mit USt-ID-Nr.: DM 353,27 zuzüglich DM 19,63 Versandkosten; Jahresabonnement EG-Binnenmarkt-Länder ohne USt-ID-Nr. und Drittländer: DM 378,– zuzüglich DM 21,– Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey GmbH & Co. KG, Spitalerstraße 12, D-20095 Hamburg, Bundesrepublik Deutschland, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde" erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Z. Säugetierkunde 59 (1994) 3, 129–192

Vol. 59 (4), 193–256, August 1994 ISSN 0044-3468 C 21274 F

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde

Verlag Paul Parey Hamburg

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

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Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologiezentrum der Christian-Albrechts-Universität, Am Botanischen Garten 9, D-24118 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

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Fortsetzung 3. Umschlagseite

 Verlag: Paul Parey GmbH & Co. KG, Hamburg. Anschrift: Spitalerstr. 12, D-20095 Hamburg, Bundesrepublik Deutschland.
Printed in Germany by Westholsteinische Verlagsdruckerei Boyens & Co., Heide/Holst.

Z. Säugetierkunde 59 (1994) 193–198

ISSN 0044-3468

Comparative ecology of the Wood mouse *Apodemus sylvaticus* in two differing habitats

By L. Canova, Lara Maistrello, and D. Emiliani

Dipartimento di Biologia Animale, Università di Pavia, Pavia and Dipartimento di Biologia Evolutiva, Università di Ferrara, Ferrara, Italia

Receipt of Ms. 27. 7. 1993
Acceptance of Ms. 28. 10. 1993

Abstract

Densities, variations in body mass, sex ratios, breeding activities and size of home-range were studied in wood mouse populations living in a woodland and a reed bed. In the reed bed population: 1. spring densities were lower, 2. body mass differed, and was lower in early autumn, and 3. home ranges were larger than in the woodland population.

It is suggested that differences in food availability and quality strongly influenced the behaviour of the two populations; the main effect of these differences was that reed bed mice entered winter with a lower body mass and suffered higher winter mortality. The larger size of the home range in the reed bed suggests that mice living in a poor-food habitat will enhance their survival by patrolling a wider area than in a rich habitat.

Introduction

Habitat features such as quality and structure, spatial heterogeneity and some related environmental parameters (availability of food and shelter and of suitable nest sites) may influence certain aspects of intraspecific rodent behaviour (Niethammer 1978; Hestbeck 1982; Wiger 1982; Gurnell 1985; Gorman and Ahmad 1993). Populations living in differing habitats may be characterized by demographic parameters such as fecundity and mortality (Krohne 1980), spacing behaviour in females (voles: Bujalska and Janion 1981) and juvenile dispersal between high- and low-quality habitats (voles: Gliwicz 1989). It is also suspected that habitat heterogeneity may partially explain the observed asynchronous fluctuation in neighbouring populations of noncyclic voles (Alibhai and Gipps 1985).

The aim of this study is to investigate wood mouse populations living in two differing habitats that are characterized by different productivity and structure: a mesic woodland and a reed bed.

Material and methods

The study was performed at the "Punte Alberete" and the "Pineta di S. Vitale" Nature Reserves, located along the eastern Adriatic coast of Italy. "Punte Alberete" is a marshland covered with extensive reed beds *Phragmites* sp. and *Carex* sp. The "Pineta di S. Vitale" biotope is a mixed spruce and deciduous woodland. The general features of the two areas, which we shall call "reed bed" and "woodland", differed strongly: arboreal cover was obviously high in the woodland, whereas in the reed bed the ground cover increased continuously from May to October in relation to reed growth. The reed bed was constantly characterized by wet soils, while in the woodland the water table decreased from May to an August minimum; the water table may sometimes rise in response to meteorological factors such as storms or rain, but usually lowers rapidly.

The study was carried out from May to October 1992. A grid of 52 Sherman traps (trapped area = 1 ha) was located in each study area and one trapping session was carried out for five days every month at each study site. The traps were baited with sunflower seeds and checked at dusk and dawn; after capture mice were weighed (g), sexed and marked by toe clipping (Twigg 1978). Each individual was aged as adult, subadult or juvenile according to fur colour and reproductive condition (Gurnell

and FLOWERDEW 1990). Reproductive conditions in males were detected by the degree of testes activity (i. e. their position in the scrotum); reproductive status for female was described as pregnant, lactating, pregnant and lactating, reproductively active (perforate vagina) or inactive (imperforate vagina).

Population abundance and home range size were estimated by the Minimum Number Alive and Minimum Area Methods (GURNELL and FLOWERDEW 1990).

Results

Population abundance and sex ratio

Seventy nine individuals were caught 172 times in the reed bed and 91 individuals were caught 187 times in woodland; the trapping effort was equal to 3120 trap checks per habitat.

Densities increased in early autumn in both habitats (Fig. 1). Throughout the study period the woodland population density was consistently higher than that of the reed bed (Mann-Whitney, U, z = 2.22, P = 0.026); however, the differences were only very marked in May and June. After June, the woodland population decreased to a minimum, while the reed bed population remained at the density attained in the late spring.

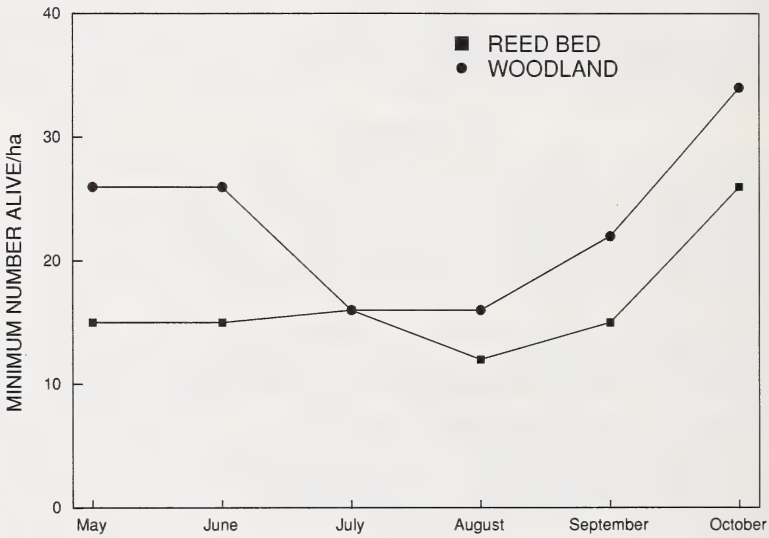

Fig. 1. Population densities in the two habitats

The adult sex ratio was biassed towards males in nearly all the months and in both habitats (Fig. 2); a slight prevalence of females was observed during June in the reed bed and in May in the woodland; only in July did the sex ratio approach parity.

Body mass variation and breeding

During the study period, variation in body mass was observed between the two populations. The weight of wood mice living in the reed bed increased rapidly from May to June and then decreased constantly up to October, whereas the woodland mice gained weight more slowly and reached their highest weight in August. The maximum weight of woodland mice was lower than that of reed bed mice and weight differences were always significant except during the July trapping session (Fig. 3).

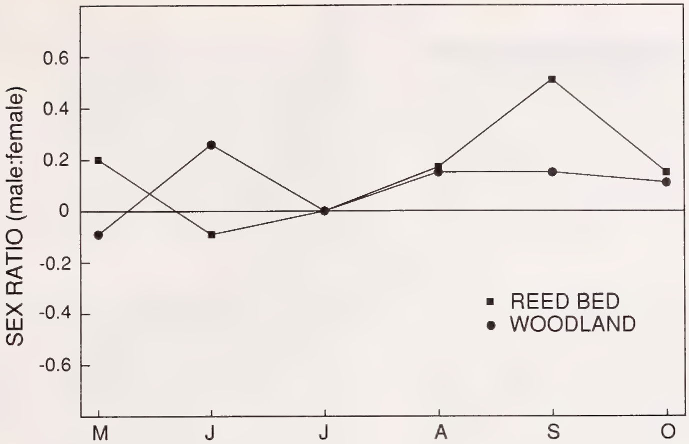

Fig. 2. Male:female sex-ratio, expressed as the logarithm of the ratio. Positive values show a male biassed ratio

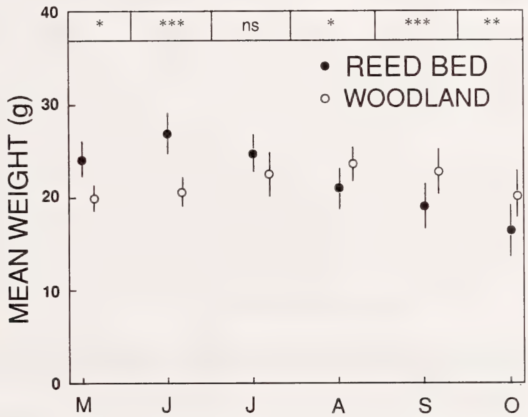

Fig. 3. Average weight (+/− SE) variations during the study period; differences were tested by Mann-Whitney U test. (* = $P<0.05$, ** = $P<0.001$, *** = $P<0.001$, ns = not significant)

At the beginning of the study nearly all the males were in sexual activity in both habitats (Fig. 4); however, in October nearly all of them entered a non-reproductive phase (abdominal testes) in the reed bed, whereas more than half the woodland males were still in a reproductive condition (scrotal testes).

A similar pattern was observed for females (Fig. 4): in the reed bed the proportion of females in a reproductive condition (perforate vagina, lactating or pregnant) was high from May to September, while in October nearly all the females were found to be in a non-reproductive condition (imperforate vagina); only one female showed the final phases of lactation activity. In the woodland, on the other hand, nearly all the females were imperforate in May and June; in October, however, ten out of fourteen females captured were pregnant or lactating.

Home-range size

Relative areas of home ranges by sex and habitat are given in the table. Because of the lack of recapture data for each trapping session we considered the average value for the home

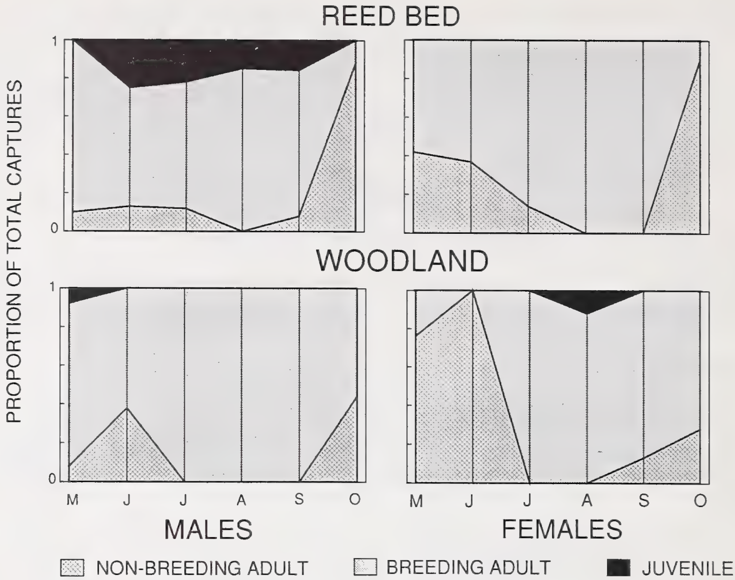

Fig. 4. Proportion of breeding and non-breeding males and females during the study period, expressed as the proportion of monthly captures

range throughout the study period. The average home-range size of reed bed mice was much higher than in woodland mice (male, Mann U, z = −4.31, $P < 0.001$; female, Mann U, z = −3.52, $P < 0.01$; from data in the table). In the reed bed the home range was significantly larger for males than for females (Mann U, z = −2.58, $P < 0.01$), whereas the home range of females was slightly larger than that of males in woodland. This latter difference, however, was not statistically significant (Mann U, z = −0.07, P = 0.93).

Home range sizes ($m^2 \pm$ SD) in the woodland and the reed bed

Differences are tested by Mann-Whitney U test

Reed bed		Woodland	
Males (8070 ± 478)	Females (6670 ± 978)	Males (4080 ± 401)	Females (4120 ± 401)

Discussion

The population trend in the two habitats follows approximately the same pattern and fits with current information concerning the reproductive biology of temperate woodland rodents (Flowerdew 1985). The autumn increases may be explained by recruitment of juveniles or subadults to the adult population. A male-biased sex ratio in both habitats is a common finding in capture-recapture studies of wood mice (Flowerdew 1985; Halle 1993), probably reflecting the polygynous social system of this rodent (Wolton and Flowerdew 1985). Several studies have shown that male home ranges overlapped those of more than one female (Brown 1969; Wolton and Flowerdew 1985). In this way males improve their chance of encountering sexually active females (Brown 1966). Moreover, in

covering a wider area they should encounter more traps compared to females and this should explain their prevalence in capture-recapture data sets.

The data from our study areas fit, at least for the reed bed, current information about sex-related differences in wood mouse home-range size.

The temporal pattern of body mass variation seems to fit the current picture of weight variation in wood mice living in temperate areas (Tanton 1969; Grodszinsky 1985). According to Grodszinsky (1985), seasonal changes in body weight are related to the dynamics of water, fat and protein content; and even though water loss and protein transformation are more involved in seasonal weight decreases than fat, the individuals that lost most weight were subject to higher winter mortality (Grodszinsky 1985). The outcome of our study may be, in conclusion, summed up as follows: in the reed bed – a habitat that may offer a lower availability of winter food since trees (and abundant seed crops) are not present – the spring density was lower, weight increased earlier, reproductive activity stopped earlier in both sexes, and male and female home-range sizes were larger than in the woodland population. In the woodland, probably as a response to better food availability, wood mice went into winter with a higher weight, stopped their reproductive activity later, maintained smaller home ranges, and reached the following spring with a higher density than the reed bed population. These last data may reflect a differential winter mortality between populations, since the October densities were not significantly different.

The differences in home-range size support the hypothesis that food availability differed between the habitats. According to a recent study (Gorman and Ahmad 1993), differences in the home-range size of mice living in contrasting habitats are related, at least in part, to differences in food quality, availability and dispersion. Differences in food availability and quality may be then an important limiting factor for the reed bed wood mice; their main effect is that the mice will enter winter with a lower body weight and will suffer higher winter mortality. Their larger home-range size suggests that mice living in a poor-food habitat will enhance their survival by patrolling a wider area than in a rich habitat.

Acknowledgements

Thanks are due to Dr. S. Vistoli (Assessorato Ambiente; Comune di Ravenna) and to C. Lazzari (Cooperativa ARCA) for permitting access to the Nature Reserve. The study was carried out with personal funds.

Zusammenfassung

Vergleichende ökologische Untersuchungen an Waldmäusen, Apodemus sylvaticus, in zwei unterschiedlichen Lebensräumen

Einige ökologische Parameter der Waldmaus wurden in zwei unterschiedlichen Lebensräumen ermittelt: in einem Nadelmischwald und in einem Marschgebiet mit *Phragmites-* und *Carex*-Bewuchs. Die Marschpopulation zeichnete sich gegenüber der Waldpopulation durch folgende Unterschiede aus: 1. Die Populationsdichte war im Frühjahr deutlich niedriger, 2. die Körpergewichte waren im frühen Herbst geringer, 3. die mittleren individuellen Aktionsräume waren größer. Daraus wird geschlossen, daß den Marschwaldmäusen weniger Nahrung bei gleichzeitig geringerer Qualität zur Verfügung stand. Die Waldmäuse in der Marsch gehen mit einem geringeren Körpergewicht in den Winter, sie unterliegen gleichzeitig einer höheren Wintersterblichkeit, was eine geringere Frühjahrs-Populationsdichte zur Folge hat. Die größeren individuellen Aktionsräume in der Marsch werden mit knapperem Nahrungsangebot in Zusammenhang gebracht.

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Authors' addresses: Luca Canova, Dipartimento di Biologia Animale, Università di Pavia, I-27100 Pavia; Lara Maistrello, Dipartimento di Biologia Animale, Università di Ferrara, I-44100, Ferrara; Davide Emiliani, cooperativa Arca, I-44030 Ravenna, Italia

Z. Säugetierkunde 59 (1994) 199–208

ISSN 0044-3468

Ontogenesis of pelage and the course of moulting in *Microtus brandti* (Radde, 1861)

By Annegret Stubbe and Sabine Wiegand

Institute of Zoology, Martin-Luther-University, Halle/Saale, Germany

Receipt of Ms. 29. 1. 1993
Acceptance of Ms. 24. 1. 1994

Abstract

Two methods are used in the investigation of the development of fur and moulting in small mammals. The most common way is to observe the pigmentation of the skin. We have used a more recent method, staining the whole animal with standard hair colours and observing changes in pelage patterns. It is thus possible to investigate ontogenetic changes in voles, and also the influences of different conditions of photoperiod and temperature on moulting. Contrary to the information in the literature, we found that newborns of *M. brandti* are pilose. During ontogenesis the following moults take place: I. Moult into the second immature pelage, II. moult into the first mature pelage, III. seasonal moultings (spring and autumn). Moults I. and II. occur, depending on the age of the animal.

Like other Arvicolidae *M. brandti* shows a sublateral course of moulting. The moult of the ventral body side is completed before the dorsal side. Deviations from this scheme, so-called "moulting variants", are possible.

Within one population of *M. brandti* the spring generation passes through five moults and the autumn generation through only four in the first year of life. Because of the shortened duration of moulting during low temperatures the first moults of the autumn generation are faster than those of spring-born animals.

These results represent a preliminary attempt to clarify conflicting observations on moulting from field investigations of small mammals, involving, in most cases, animals of different age classes and generations from one population.

Introduction

Investigations concerned with moulting are rare. At the beginning of this century, studies of mammalian pelt were undertaken mostly because of the commercial use of hunted game furs. Initial results were obtained from mammals that changed their fur colour. Later, the connection between moult and the state of pigmentation of the inner surface of skin was discovered. Continuous observations of hair changes in living animals are still rare, but they still offer the best opportunity for investigating the postnatal ontogenesis of moulting under different environmental conditions. We examined the moulting processes in the vole *Microtus brandti*, because of their ease in keeping, their highly developed social behaviour and our rather good knowledge of this species. The aim of the present study was to establish a general model of the moulting processes in small rodents, especially Arvicolidae.

Material and methods

Species and maintenance conditions (MC)

The vole *Microtus brandti* is a very social animal, living in large colonies and often exhibiting cyclic fluctuations and gradiations in its abundance. The species occurs throughout the steppes of Central Asia and has extended its distributional area eastwards in recent years. The vole shows a high reproductive potential and, as a diurnally active herbivore, is regarded as the most important competitor of pasture animals.

In our laboratory, voles were bred in a HAN-rotation system for rigorous outbreeding (Rapp 1982) and were kept under standard environmental conditions (21 ± 2 °C, 50–60 % humidity, L:D =

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14:10, L_{on} 4.00 a.m., light intensity ≈ 300–400 Lux). After weaning at an age of 21 days, the animals were kept in sibling groups. For these investigations voles were maintained under different conditions (MC):

MC 1: 21 ± 2 °C, L:D = 14:10 (L:D, T = const.)
MC 2: 20 ± 2 °C, L:D adapted to the natural photoperiod (L:D ~, T = const.)
MC 3: T and L:D adapted to the natural changing conditions (L:D, T ~)
MC 4: 20 ± 2 °C, LL (light throughout the day).

Feeding was the same for all animals: standard pellets and water ad lib., plus fresh food (apples, carrots, cabbage, *Taraxacum*) three times each week.

Staining and pelt investigations

To investigate moulting we used a treatment modified from MILITZER (1989). Animals were anesthetized by using a 1.43 % solution of sodiumhexobarbital and then stained with standard hair colouring (LONDANCOLOR, black). Following completition of one moult, the voles were re-stained. Changes in pelage patterns were recorded weekly. For each MC, twenty animals were investigated over a timeperiod of one year. We distinguished between a spring generation (animals born in spring) and an autumn generation (animals born in late summer or autumn). To complete these studies, we observed the skin pigmentation of dead animals from the laboratory, and also from those caught between 1988 and 1990 in their natural environment near Ulan-Bator (Mongolia).

Results

Genesis of neonatal pelage

The following results are based on observations of 22 animals born in three litters. Voles are born with eyes and ears closed, and only the vibrissae are visible without the microscope; they seem to be naked. Contrary to the opinion in the relevant literature, the whole body excluding the soles is covered with short, fine hairs after birth (Fig. 1, 10 min. after birth, umbilical cord not bitten through at this time).

Table 1 gives an overview of the genesis of neonatal pelage.

Fig. 1. Skin surface of a newborn *Microtus brandti*, 10 min. post partum

Postnatal ontogeny of fur development and moulting

After the first juvenile pelage, voles moult into a second juvenile coat and then into the mature pelage, which may be a summer or a winter fur, depending on date of birth and season. Spring-born animals pass through five moults, because the first mature coat is a summer fur. They change into a winter pelage in autumn, whereas the autumn generation

Table 1. **Genesis of hair coat**

Day of life	Appearance
2.	whole animal covered with downy hair, especially dorsal side and on the back of the head
3.	DS down to the top of the feet darker, VS more light coloured, vibrissae growing
5.	forefeet pilose
6.	hairs begin to grow in length (2 mm)
7.	hind feet pilose, body hairs 3 mm long
8.	vibrissae 10 mm, hairs on DS 4 mm, with some dark pile hairs in between, VS hairs 3 mm long
9.	portion of pile hairs growing, eyes start to open (up to 11^{th} day of life)
10.	vibrissae 13 mm, DS with underwool
12.	eyes and ears open, VS with good visible underwool, DS with longer pile hairs
15.	VS hairs 5 mm long, vibrissae 15 mm long, pile hairs rising above the coat
12.–15.	development of first juvenile pelage (development of new hairs) is complete, after 15^{th} day no skin pigmentation was found, hairs only growing in length up to 23^{rd} day
17.	vibrissae 20 mm
20.	vibrissae 30 mm
23.	DS and VS hair length 5 mm, woolly hairs and guard hairs are fully grown, so pile hairs are no longer above the rest of the coat

VS = ventral side, DS = dorsal side of animal.

Table 2. **Frequencies of moulting variants**

Variants	Number (n)	Frequency (%)
Dorsal A	204	51.64
Dorsal B	17	4.31
Dorsal C	71	17.97
$\text{Dorsal}_{\text{diff}}$	103	26.08
total	395	100.00
Ventral A	53	13.45
Ventral B	216	54.82
$\text{Ventral}_{\text{diff}}$	125	31.73
total	394	100.00

moults into a winter coat with the first adult fur in the first year of life. All animals living under changing environmental conditions, and born in spring develop a second winter fur. Thus, the autumn generation undergoes only four moults in the first year.

For better understanding we defined the different courses of moulting as "variants". Excluding the moultings of senescence, *Microtus brandti* generally shows a synchronous growing of hairs. To allow systematic observation of moulting we have regarded the dorsal and ventral body surfaces as independent, although they are both one entity in moulting. The moult generally begins ventrally and advances over the flanks to the back; therefore it is completed ventrally earlier than dorsally. This course is defined as sublateral moulting by Kryltzov (1964). Figure 2 shows the variants of ventral moulting (A – beginning laterally and forming a band, B – beginning cranially and at the axillae; both ending at the feet and tail). Figure 3 explains the dorsal variants; all three start at the shoulders and

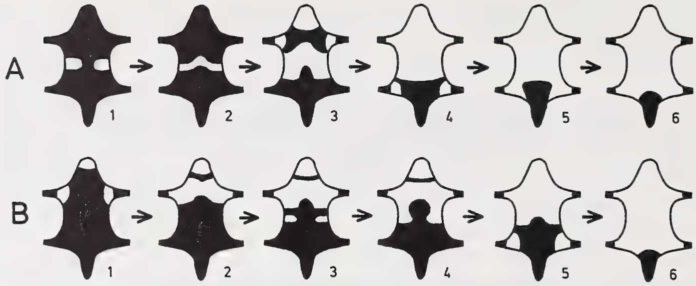

Fig. 2. Moulting variants of the ventral side, black: old coat, white: new pelage

haunches and end at the tail. Dorsally as well as ventrally the paws moult least or are excluded from the moult. The tail may also show irregularities, such that we found a "raccoon-like" marking, although the tail is always completely moulted. These described moulting variants were observed in all ontogenetic hair changes (excluding senescence) and, under each maintenance condition. They seem to be independent of abiotic factors or birth date, suggesting they may be endogenous. Table 2 shows the recorded dorsal and ventral body side variants of moulting and their frequencies. The variants $Dorsal_{diff}$ and $Ventral_{diff}$ comprise patterns, which cannot be categorized within the described variants above, and include the scattered moultings of senescence. Table 3 explains the frequencies of the observed variant combinations. Through its life time one animal can change from one moult variant combination to another. We observed that, in most cases, the first moults show other combinations than the later ones. The following changes occurred:

Table 3. **Combinations of variants and their frequencies**

Variants Dorsal/ventral	Number (n)	Frequency (%)
A/A	28	11.72
A/B	134	56.07
B/A	2	0.83
B/B	10	4.19
C/A	11	4.60
C/B	54	22.59

AA $\longrightarrow$ AB, BB, CA, CB
AB $\longrightarrow$ AA, BB, CA, CB
BB $\longrightarrow$ AA, AB
CA $\longrightarrow$ CB
CB $\longrightarrow$ AA, AB, CA

Moultings of senescence (scattered moultings)

With increasing age ordered moulting begins to change to scattered patterns. Animals of higher age no longer show regular moults (Fig. 4). Normally, such a scattered moulting pattern was recorded after the first year of life, but it can also occur earlier; thus the first irregular moults can be observed in animals which are six or seven months old. These diffuse hair changes are included in the seasonal moults and are not separate entities.

Influence of age on the moulting process

Under defined maintenance conditions (MC) the start and the end of the moults from first to second juvenile pelage and from the second to the mature coat occur very close together for all animals. These dates seem to be more strongly correlated with age than the subsequent (seasonal) moultings. Figure 5 shows the duration of the spring (S) and autumn

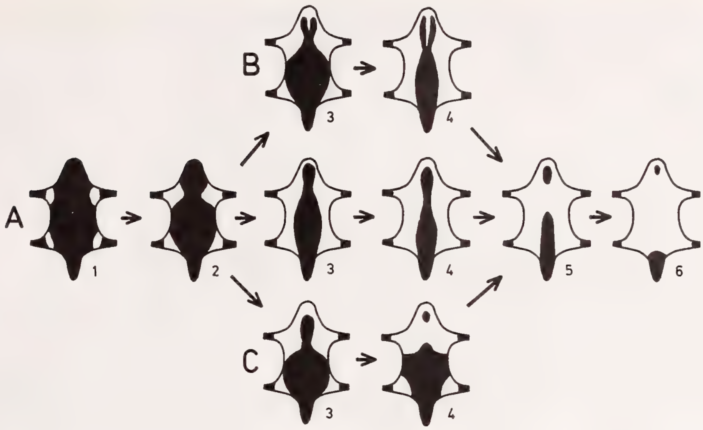

Fig. 3. Moulting variants of the dorsal side, black: old coat, white: new pelage

Fig. 4. Examples of scattered moulting; above dorsal side, below ventral side

(A) moults of animals under different maintenance conditions (MC 1, 2, 3). The first hair changes begin between the 28th and 37th day, and end between the 37th and 71th day of life. The average duration is twenty days (average between 31th to 50th day of life, dark bars within the white and structured in figure 5). Comparing the average durations of juvenile moults within the spring or autumn generation, they are nearly equal under all maintenance conditions. The spring generation simply takes longer to moult into the second juvenile coat than the autumn-born animals. Moulting into the mature fur requires the longest period (35 days for the autumn generation, 50 days for the spring generation). It starts between the 51st and 111th day of life, and finishes between the 139th and 215th day (average: start 81st to 120th, end 122nd to 158th day). Again, the autumn generation moults more rapidly than spring-born animals. The animals in MC 3 (LD, T ~) are the first to start and finish the hair changes influenced by temperature and photoperiod, whereas the animals of MC 1 (L:D, T = const.), without any "zeitgeber", show the latest dates and the largest variation in moulting times. Therefore, the moult from first into second juvenile fur seems to be very closely connected with a defined age, whereas moulting into the mature coat is influenced by day length and temperature as are, to a greater extent, the subsequent seasonal moults.

Table 4 shows the results of various authors for the commencement and the end of the first and second moults during postnatal ontogenesis in Arvicolidae and Muridae (after Bühlow 1970, completed).

Table 4. **Commencement and end of moulting into the second juvenile and into the first adult coats of some Arvicolidae and Muridae**

Authors		Species	First into second juvenile coat Age (days) Start	End	Second juvenile into first mature coat Age (days) Start	End
Becker	(1952)	*Rattus norvegicus*	42	84	75	–
Borum	(1954)	*Mus musculus*	30	46	60	–
Collins	(1923)	*Peromyscus maniculatus*	28	56	60	–
Dry	(1926)	*Mus musculus*	18	35	45	–
Ecke and Kinney	(1956)	*Microtus californicus*	25	45	60	–
Frank and Zimmermann	(1956)	*Microtus oeconomus*	–	56	–	–
Fullagar	(1967)	*Apodemus sylvaticus*	35	50	56	–
Fullagar	(1967)	*Apodemus flavicollis*	–	–	63	–
Kästle	(1953)	*Micromys minutus*	28	44	–	–
Kemper	(1976)	*Pseudomys novaehollandiae*	–	–	35	105
Langenstein-Issel	(1950)	*Pitymys subterraneus*	–	50	–	–
Linzey and Linzey	(1967)	*Ochrotomys nuttalli*	31	87	–	–
Mazak	(1962)	*Clethrionomys glareolus*	30	75	–	–
McManus and Zurich	(1972)	*Meriones unguiculatus*	32	55	58	112
Militzer	(1987)	*Mesocricetus auratus*	–	111	112	155
Stein	(1960)	*Microtus arvalis*	23	54	59	–
Sykora	(1959)	*Microtus arvalis*	20	–	–	–
Viitala	(1981)	*Clethrionomys rufocanus*	26	60	59	88
Stubbe and Wiegand	(this study)	*Microtus brandti*	31	50	81–120	122–158

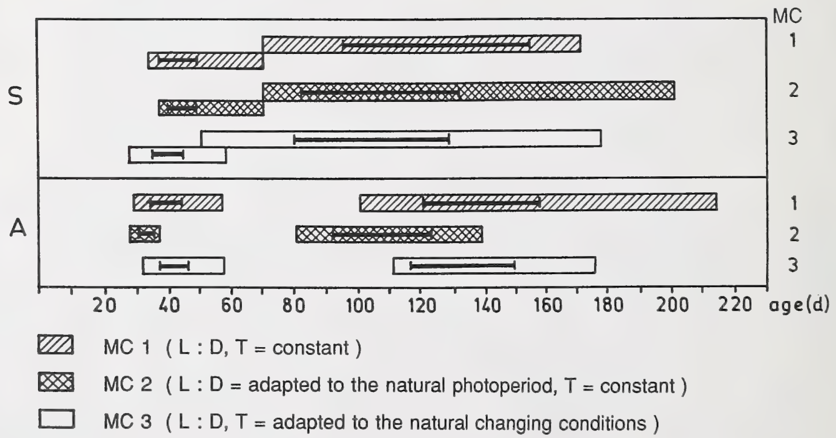

Fig. 5. Start and end of age-dependent juvenile moults; S: spring generation, A: autumn generation

Comparative studies on pelts

In addition to the observations on living animals, we have also investigated pelts of dead animals (N = 1158, MC 1 – n_1 = 728, MC 2 – n_2 = 330, pelts of animals caught in Mongolia – n_3 = 100).

The results of both methods agree completely, but with stained living animals it is possible to follow all moults through the life of one animal and, in the end, we required about 7000 voles less for the present study by staining the animals as we had used only the old method to observe skin pigmentation. Figure 6, for example, shows some typical patterns of juvenile moulting of killed animals. Hair replacements are visible in the epidermis by the pigment production of melanocytes, which were accumulated before the hair follicles maturate (RYDER 1973). The colour of the pigmentation is therefore extremely dark in the areas of active hair growth and becomes lighter as the hairs change and growth ceases (VIRO and KOSKELA 1978). Figure 6 shows the beginning (left), middle and end phases (right) of the second juvenile moult. The left picture conforms with variant A2, the middle with A3 and the right with A5 from figure 3.

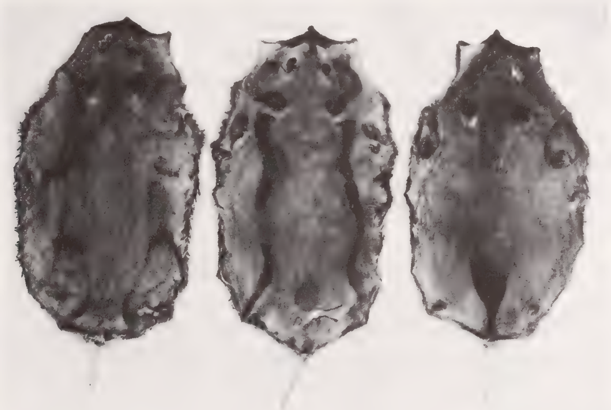

Fig. 6. Typical skin patterns of juvenile moultings; left: start, right: endphase of moult

Discussion

According to many mammalogists, neonates of small rodents are born with a nude body surface except for the vibrissae, 1 to 2 mm in length (TOLDT 1935; NIETHAMMER and KRAPP 1978, 1982). BAKE (1981), SYKORA (1959) and STEIN (1960) reported on *Microtus arvalis* that the first hair tips appear on the second day of life. For *Pitymys subterraneus* LANGENSTEIN-ISSEL (1950) stated that, on the day of birth, 0.5 mm long, light hair tips can be seen under a magnifier. SCHRÖPFER (1977) found the first hair fuzz on the dorsal side on the third day of life and sinus hairs one day earlier. FRANK and ZIMMERMANN (1956) observed the first dark hairs in *Microtus oeconomus* on the second day of life. COLLINS (1923) also determined this date for the genus *Peromyscus*. In *Microtus agrestis* the hair colouration is visible on the fourth day of life (NIETHAMMER and KRAPP 1982). For *Micromys minutus* opinions vary: SLEPSOV (1947) observed the first hairs on the fourth day and KÄSTLE (1953) on the second day of life.

We have studied newborn *Microtus brandti* 10 minutes after birth, and by use of a binocular microscope observed sparse, small hairs over the entire body surface, as well as vibrissae. This differs from the general opinion; only KOURIST (1957) also described

colourless hairs over the entire body a few hours after birth in *Cricetus cricetus.* It is our opinion that the type of hair development noted in *Microtus brandti* is also common in other Arvicolidae; we also found it in *Alticola semicanus,* the high mountain vole.

The genesis of neonatal pelage seems to be comparatively uniform; we only observed individual variations of 1 or 2 days. The representation given may be a general guide to the genesis of first juvenile pelage, not solely in *Microtus brandti.* The following authors gave the same developmental states: LANGENSTEIN-ISSEL (1950) delimited the end of development of the neonatal coat of *Pitymys subterraneus* between 12 and 14 days; BAKE (1981), FRANK and ZIMMERMANN (1956), STEIN (1960) and SYKORA (1959) cited the 14th day for *Microtus arvalis* and KÄSTLE (1953) the 15th for *Micromys minutus.*

Hairs have a limited life span. After the duration of the growth process, they die and are rubbed off during moulting. TOLDT (1935) distinguished between the periodic or seasonal moults which occur in wild mammals of cold and temperate zones, and the continuous (partial) moults of domesticated animals and humans. According to TOLDT (1935) animals of tropical and arctic zones, or adapted to aquatic habitats, show only one moult per year. A companion paper to this publication (STUBBE and WIEGAND 1994) will deal with seasonal moults in *Microtus brandti.*

Concerning the course of moulting, synchronous and asynchronous hair growth has been described. In *Microtus brandti* we found synchronized hair growth. KRYLTZOV (1964) noted sublateral moulting, with only minimal variations, in 18 species of Arvicolidae, LANGENSTEIN-ISSEL (1950) for *Pitymys subterraneus,* and ECKE and KINNEY (1956) for *Microtus californicus.* In evolutionary terms all these are comparatively "young" species. Primitive genera change their hair coat according to other patterns; *Clethrionomys,* in particular, shows the so-called cephalo-sacrale type. In *Microtus brandti* the sublateral type of moulting was corroborated and described from the investigation of stained living animals.

The scattered moulting of senescence has been observed by various authors: BAKE (1981) described this for 9- to 15-month-old *Microtus arvalis,* COLLINS (1918) – *Peromyscus* spec.; BECKER (1952) – *Rattus norvegicus,* ESPAÑA et al. (1985) – *Mus spretus;* BÜHLOW (1970) – *Arvicola terrestris;* and KRYLTZOV (1964) for some *Microtus* species. OLIVEIRA et al. (1992) found different pelages in sexually active males and females of *Marmosa incana,* but did not note any influence of seasons. ROWSEMITT et al. (1975) found a relationship between diffuse moulting and reproductive activities, but we have the impression that gravidity simply accelerates normally occuring moults. Generally, ageing processes were considered a primary premise of irregular moults. This is also our opinion, derived from observations on animals kept under MC 4 (T = const., LL), which age more rapidly than other voles because of light stress, and already show scattered moulting patterns within 5 months.

There is general agreement with regard to the induction of juvenile moults. Our observations show that the changes from first to second juvenile, and from there to the first mature coat, are not dependent on season, but we did find a close correlation between age and the start of these moults.

From a comparison of *Microtus* species a high correspondence of dates is evident, and the results from *Microtus brandti* also coincide closely. This high conformity, and the small possibility of the influence of exogenous factors, indicate the probability of an age-dependent course in juvenile moults. These results agree with those of LANGENSTEIN-ISSEL (1950), STEIN (1960) and VIITALA (1981). VIITALA (1981) refered to the influence of exogenous factors (temperature) on the duration of moults, and from keeping animals under different temperature regimes in the laboratory. Animals under colder conditions changed their hair coat faster than animals in warmer environments.

In our study, we found moult duration to be dependent on birth date (spring or autumn) and on abiotic factors (day length and temperature). The influence of abiotic

factors on juvenile moults, however, is not as strong as in the subsequent adult moults. The seasonal dependence of mature hair changes will be discussed in the companion paper (STUBBE and WIEGAND 1994).

Acknowledgements

This publication is no. 225 of the "Results of Mongolian-German Biological Expeditions since 1962".

We thank Dr. H. GRIFFITHS from the Department of Genetics of the University of Leeds for linguistic corrections.

Zusammenfassung

Ontogenese des Haarkleides und Fellwechselverlauf von Microtus brandti (Radde, 1861)

Neben dem üblichen Verfahren, den Fellwechsel bei Kleinsäugern anhand der Pigmentierung der Hautunterseite abgebalgter Felle zu beurteilen, wurde mit Hilfe der Methode des Einfärbens der Tiere mit einem herkömmlichen Haarfärbemittel und der wöchentlichen Aufzeichnung der entstehenden Fellmuster eine Beobachtung des Mausergeschehens am lebenden Tier möglich. Somit konnte nicht nur der Mauserverlauf während der Ontogenese, sondern auch der Fellwechsel bei Einfluß der Photoperiodik und von Temperaturänderungen an ausgewählten Tieren über längere Zeiträume beobachtet werden.

Entgegen der in der Literatur vertretenen Auffassung wurde erstmals eine Behaarung neugeborener Tiere nachgewiesen. Innerhalb der Ontogenese treten folgende Härungen auf: I. Fellwechsel in das 2. Jugendkleid, II. Fellwechsel in das 1. Alterskleid, III. saisonale Haarwechsel (Frühjahr und Herbst). I. und II. verlaufen altersabhängig.

Insgesamt zeigt *Microtus brandti* wie auch andere Arvicolidae einen sublateralen Mauserverlauf. Der Fellwechsel der Ventralseite ist eher abgeschlossen als der der Dorsalseite. Abweichungen von diesem Schema, sogenannte „Mauservarianten", sind möglich. Innerhalb einer Population durchläuft die Frühjahrsgeneration fünf, die Herbstgeneration nur vier Haarwechsel im ersten Lebensjahr.

Die vorliegende Studie möchte zur Klärung der sich häufig widersprechenden Beobachtungen des Fellwechsel bei im Freiland gefangenen Kleinsäugern beitragen, die durch den gleichzeitigen Fang von Tieren verschiedener Altersklassen und Generationen entstehen können.

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Authors' address: Dr. Annegret Stubbe and Dipl.-Biol. Sabine Wiegand, Institut für Zoologie, Martin-Luther-Universität Halle-Wittenberg, Domplatz 4, D-06099 Halle/Saale, FRG

Z. Säugetierkunde 59 (1994) 209–217

ISSN 0044-3468

Reproductive biology and population structure of *Rattus rattus* in Rawalpindi, Pakistan

By J. E. Brooks, E. Ahmad, and I. Hussain

Denver Wildlife Research Center, Denver, Colorado, USA and Vertebrate Pest Control Project, National Agricultural Research Centre, Islamabad, Pakistan

Receipt of Ms. 4. 11. 1993
Acceptance of Ms. 24. 3. 1994

Abstract

Studied the breeding biology and population structure of roof rats (*Rattus rattus*) in the wholesale grain and commodities market in Rawalpindi, Pakistan. Rats were trapped from the grain market monthly for 14 months. We necropsied 2327 rats, comprising 1175 males and 1152 females, essentially a 1:1 sex ratio. Males were found fertile in every month, with no significant seasonal differences; females were pregnant in every month, and the adjusted frequency of pregnancy averaged 39.8 %. Litter size during the last quarter of pregnancy averaged 6.1 ± 1.7 Standard Deviation (SD). Based upon primiparous and multiparous females, we calculated that an average adult female had 1.8 pregnancies. Average production of young was 10.9/female (6.1 × 1.8). Immature animals (weaned, but not sexually mature) constituted 13.1 % of the total collection, and recruitment was continuous during the study, indicating high mortality among nestling and weanling rats. Numerous wounds and scars on adults of both sexes indicated a high degree of social strife and aggression among the rats.

Introduction

The rat commonly found in grain storage facilities, wholesale commodities markets, cities, towns, and farm houses in Pakistan is the roof rat (*Rattus rattus*). Taber et al. (1967) refer to the subspecies in the Indus Plains and upland areas in northern Pakistan as *R. rattus rufescens* (Gray), a brownish-gray-backed form with a venter either creamy white or light gray with a rufous tint. The typical mammary formula is 2 + 3 = 10, with an occasional pairing of the postaxial mammae to give a 3 + 3 = 12 formula.

Previous studies dealing with the reproductive biology and population dynamics of this subspecies in similar habitats gave somewhat contradictory findings. Beg et al. (1983) in Faisalabad, Pakistan, found that trapping success was lowest in winter and peaked in summer: pregnancy occurred only in 10 months of the year and averaged 45 % during the study; the proportion of young was highest in the winter and averaged 31 % of the collections during the year. Rana et al. (1983) in Jodhpur, India, found that females were pregnant throughout the year; the annual frequency of pregnancy was 25.5 %; the proportion of young averaged 54 % and was lowest from January to April. Additional information on the reproductive biology and population dynamics of this subspecies is needed to use control methods with proper timing. Thus, we carried out a 14-month study of the roof rat population in the wholesale grain market in Rawalpindi, Pakistan.

Material and methods

Description of the grain shops

The Rawalpindi market consists of several hundred dealers occupying ground floor, small (25 m^2–45 m^2 floorspace) shops, 40–50 years old, with capacities for 500–800 bags of commodities (50–80 metric tons). None of the shops are ratproof. The main commodity is rice; other foods available are

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lentils, grams, sorghums, wheat flour, and groundnuts. The amounts of grains sold annually vary from 1,000 bags to 60,000 bags (Brooks et al. 1987).

Trapping

Commercial wire-mesh live traps (41 × 14 × 14 cm) and Sherman galvanized steel traps (25 × 7.5 × 8 cm) were used. The smaller traps were more suitable for smaller rats. We baited the traps with fresh seasonal vegetables or fruit, which the rats readily accepted, and trapped for 4 consecutive nights each month from April 1987 through May 1988 by setting ten wire-mesh traps and five Sherman traps in each of eight shops. Each month we selected eight different shops, four on each side of the roadway, to minimize invasion from surrounding shops and to avoid the effect of removal trapping on population size. The Sherman traps were not available during the first 2 months of the study.

Necropsy procedure

After using chloroform to kill rats in the laboratory, we necropsied 2327 rats. Slight discrepancies in totals resulted when all data were not taken on some rats. We weighed and measured each animal before necropsy and recorded reproductive data: for females, this included the condition of the vaginal orifice (perforate or not), condition of the uterus (nulliparous, pregnant, placental scars), condition of the ovaries (corpora lutea visible or not), number of embryos, their crown-rump length, and whether any were resorbing. For males, we recorded the position (abdominal or scrotal), length, and weight of testis, and whether the tubules of the cauda epididymis were visible or not. We recorded the number of scars, wounds, fractures, and missing limbs on the trapped rats.

We classified animals as sexually mature by calculating the 50 % points at which females showed visible corpora lutea and males showed visible tubules in the cauda epididymis (Davis 1964). Animals meeting or exceeding these 50 % points in body weight (BW) and in head and body length (HBL) were adults; all others were immatures.

Using Harrison's (1952) methods to compare rat populations, we calculated the "embryo rate" (the crude pregnancy rate × the unadjusted embryo number = the number of embryos per 100 females of all sizes) and the "reproduction rate" (the number of embryos per 100 head of population, males and females). We believe these rates to be more indicative of a population's reproductive potential than the reproductive rate as defined in Southwick's (1966) procedure in which he used the yearly production per female, calculated from the average litter size and the incidence of pregnancy (yearly pregnancies per female). The incidence of pregnancy is an artificial figure indicating the number of times a female rat could be pregnant during a year; actually very few female rats live a year, so the incidence of pregnancy gives an overestimation of potential production. We used 16 days as the period of visible pregnancy in the roof rat (Southwick 1966).

Population estimates

Monthly population estimates were calculated from the linear regression of cumulative captures on daily captures (Blower et al. 1981). Because captures were taken from a different set of eight grain shops each month, we cannot generalize much about seasonal population changes. We compared the number of animals captured with population estimates to see if there was a correlation.

Results

Characteristics of the sample

The proportion of males to females was 50.5:49.5, which does not differ significantly from a 1:1 sex ratio. Males grew to a greater body weight than did females, but did not exceed females in head and body length (Tab. 1). There was no significant difference in mean body weight at equivalent HBL's between sexes below 160 mm; above that point, males were significantly heavier ($P = 0.01$). Males predominated in the largest size classes. The largest male weighed 273.5 g and measured 214 mm. The heaviest female weighed 246.8 g and measured 199 mm; however, the longest female measured 215 mm. The mean weight of pregnant females was 163.2 g ± 29.5, ranging from 84.4 to 246.8 g.

Table 1. **Head and body length (HBL), body weight (BW), and sex ratio of *Rattus rattus* from Rawalpindi, Pakistan**

(Mean ± SD)

Head and body length size classes (mm)	Males		Females		
	Number of animals	Body weight (g)	Number of animals	Body weight (g)	*P*
80– 89	1	18.5	3	18.0 ± 1.7	ns
90– 99	12	24.6 ± 2.9	13	23.9 ± 3.5	ns
100–109	18	34.2 ± 3.8	23	32.9 ± 4.3	ns
110–119	12	40.3 ± 6.6	18	44.1 ± 6.9	ns
120–129	29	51.8 ± 10.2	27	53.7 ± 7.2	ns
130–139	21	67.8 ± 11.5	29	65.8 ± 10.9	ns
140–149	53	88.6 ± 12.5	73	86.5 ± 11.0	ns
150–159	102	106.0 ± 13.7	102	103.3 ± 13.2	ns
160–169	158	127.9 ± 17.5	192	122.9 ± 14.4	0.01
170–179	296	150.1 ± 18.5	308	146.0 ± 17.4	0.01
180–189	286	170.9 ± 20.1	235	166.1 ± 18.9	0.01
190–199	150	191.8 ± 23.1	109	176.6 ± 18.3	0.01
200–209	34	205.0 ± 19.9	18	181.9 ± 23.6	0.01
210–219	3	231.3 ± 43.2	2	206.4 —	—
Totals	1175		1152		
Means, BW	146.8 ± 51.3		138.1 ± 46.7		
Means, HBL	171.4 ± 21.3		167.9 ± 22.0		

Reproduction

We defined mature females as those that weighed ≥80 g or were ≥139 mm in HBL; mature males weighed ≥96 g or were ≥152 mm in HBL. We observed fertile males in every month of the year. Male fertility begins when testis weight reaches 0.7–0.8 g and a length of 16–17 mm. Many males with testis smaller than these nevertheless were observed to be scrotal. There was little seasonal fluctuation in mean testis weights when adjusted for mean body weights (Fig. 1).

The adjusted frequence of pregnancy, as judged by visible pregnancy in all adult females (≥80 g BW), ranged from 30 % in April to 58 % in July (Fig. 2). The frequence of

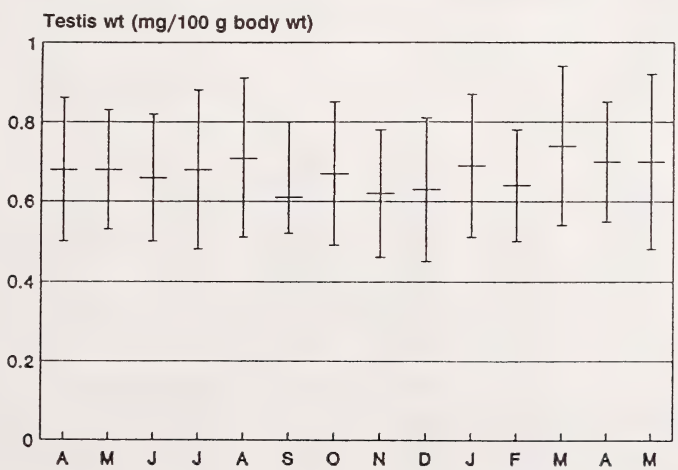

Fig. 1. Mean testis weights (± SD) in male *R. rattus* adjusted for monthly body weights

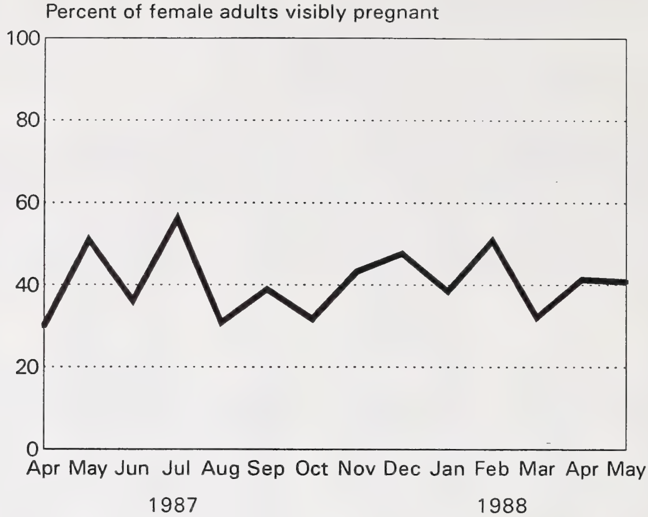

Fig. 2. Percentage of visible pregnancies monthly in adult female *R. rattus*

pregnancy for the entire study was 39.8 %. The smallest pregnant female was 145 mm HBL, but most pregnancies occurred in females ≥ 150 mm HBL and ≥ 100 g body weight (Tab. 2).

Primigravid females constituted 53.7 % of all pregnancies (Tab. 3). The 1:0.78 ratio between females pregnant for the first time and those bearing their second litter indicates that, on the average, primigravid females have a 78 % chance of living long enough to have a second pregnancy.

Litter size

The number of embryos per female ranged from 1 to 16, and 80 (3.0 %) of the total of 2682 embryos were resorbing. We examined litter size by embryo size (CR = crown-rump length), roughly corresponding to the second, third, and fourth quarters of pregnancy, and

Table 2. **Relationship of HBL and BW to visible pregnancy in female *R. rattus* from Rawalpindi**

Body size class (mm)	Number examined	Pregnant Number	%	Body weight class (g)	Number examined	Pregnant Number	%
<140[a]	113	0	0.0	<80[a]	131	0	0.0
140–149	73	4	5.5	80– 99	88	5	5.7
150–159	102	29	28.4	100–119	116	24	20.7
160–169	192	88	45.8	120–139	191	64	33.5
170–179	308	123	39.9	140–159	229	93	40.6
180–189	235	103	43.8	160–179	214	105	49.1
190–199	109	53	48.6	180–199	117	66	56.4
200–209	18	5	27.8	200–219	54	37	68.5
210–219	2	1	50.0	220–239	12	12	100.0
Total rats							
≥ 140 mm	1039						
≥ 80 g					1021		
Total/percent rats pregnant		406	39.1			406	39.8

[a] Immatures.

Table 3. **Corpora lutea and parity in *R. rattus***

HBL size class (mm)	Number examined	Corpora lutea visible	Nulli-parous	Primi-gravid	Multi-gravid	Parous Non-gravid with scars 1 set	2 sets	3 sets
80– 89	3	0	3	0	0	0	0	0
90– 99	13	1	13	0	0	0	0	0
100–109	23	1	23	0	0	0	0	0
110–119	18	1	18	0	0	0	0	0
120–129	27	6	27	0	0	0	0	0
130–139	29	12	29	0	0	0	0	0
140–149	73	58	63	4	0	6	0	0
150–159	99	95	51	24	5	19	0	0
160–169	188	186	34	69	19	53	13	0
170–179	299	293	25	59	64	95	52	4
180–189	228	225	10	42	61	50	58	7
190–199	107	107	5	17	36	17	27	5
200–209	17	15	3	3	2	4	5	0
210–219	2	2	0	0	1	1	0	0
Totals	1126	1002	304	218	188	245	155	16

found that embryo counts in the second quarter averaged 6.90/female and decreased to 6.09/female in the last quarter. This decrease indicated an intrauterine loss of 0.81 embryo, a mortality of 11.7 % of embryos from all causes. Litter size changed with increasing body size of the female from 5.7 ± 1.8 (in females 150–159 mm HBL) to 7.4 ± 2.0 (in females 190–199 mm HBL).

Population and age structure

Sex ratios from immature and adult rats were basically alike, although males predominated among the immature rats (142 males to 123 females), but the difference was not significant (X^2 = 1.36, P = 0.20). Data for April and May 1987 were not used because the smaller traps suitable for immature rats were not available then.

The recruitment of young animals into the population occurred throughout the year (Tab. 4). We found that recruitment of immatures each month showed a significant correlation with the frequence of pregnancy in the preceding month (r = 0.742, t = 3.5, P = 0.005).

Table 4. **Recruitment of young *R. rattus***

Month	Immatures	Adults	% immatures
Jun.	31	145	17.6
Jul.	22	168	11.6
Aug.	21	108	16.3
Sep.	18	180	9.5
Oct.	14	124	10.1
Nov.	7	126	5.3
Dec.	25	168	12.9
Jan.	17	95	15.2
Feb.	27	133	16.9
Mar.	21	115	15.4
Apr.	15	102	12.8
May	26	158	14.1
Totals	244	1622	13.1

April and May 1987 captures are deleted because small live traps for immature rats were not available in those months.

Population estimates

Except for April 1987, the captures per trap night varied only between 0.24 and 0.41 (Tab. 5). The capture rate and numbers of animals removed were virtually the same in June 1987 and May 1988. This is indicative of stable populations; most differences in population estimates occurred because of trapping vagaries, (e.g., more rats captured on the second or third night, or disturbances in shops that may have affected captures). There was a fair correlation between the number of animals captured and the estimated population (power regression, correlation coefficient = 0.64).

Table 5. **Roof rat captures, trap success, and estimated populations from Rawalpindi**

Month	Captures/day 1	2	3	4	Total captures	Trap nights	Captures/ trap night	Estimated population
Apr. 87	63	59	53	45	220	320	0.69	785
May	45	23	21	21	110	320	0.34	149
Jun.	51	53	39	33	176	480	0.37	389
Jul.	51	57	42	40	190	480	0.40	573
Aug.[a]	43	39	24	23	129	420	0.31	210[a]
Sep.	54	48	52	44	198	480	0.41	1034
Oct.	35	44	29	30	138	480	0.29	455
Nov.	43	40	27	26	136	465	0.29	254
Dec.	46	61	43	43	193	465	0.41	908
Jan. 88	35	34	28	15	112	465	0.24	191
Feb.	41	42	40	37	160	480	0.33	1239
Mar.	36	39	36	25	136	480	0.28	407
Apr.	36	34	31	16	117	465	0.25	211
May	45	50	47	42	184	480	0.38	1850
Totals	624	623	512	440	2199	6280	0.35	8655

[a] 7 shops only.

Table 6. **The frequence of scars, wounds, and missing body parts in *R. rattus***

Disabilities	Females	Males
Part of tail gone	125	194
Wounds on tail	58	76
Fracture of tail	15	17
Swollen tail	4	1
Wounds or abscess on body	20	13
Wounds or swollen legs	5	2
Fracture of hind foot	1	0
Missing hind leg	0	1
Totals	228	304

Intraspecific strife

The most frequently observed evidence of fighting among the rats was that parts of tails were missing (Tab. 6). Wounds on tails were seen next in frequence. In aggressive encounters among rats, the winner quite often bites at the lower back or tail of the loser (personal observation). Fractures and swellings of tails were seen less often. Many females were wounded and had missing body parts (18 % of the total female sample). This is indicative of extreme strife since aggressive exchanges are usually confined to those between males (Barnett 1963). Altogether, animals bearing evidence of aggressive exchanges were about 23 % of the total collection.

The incidence of injuries increased sharply for rats of both sexes ≥ 150 mm in body size. This could be due to cumulative encounters.

Discussion

We compared our findings with those of two similar studies cited earlier. The sizes of rats at maturity depend on the average body sizes of rats in each population. The average sizes of rats differ in the three populations: Faisalabad females averaged 87 g and males averaged 94 g; Rawalpindi females averaged 138 g and males averaged 147 g. Roof rats from Jodhpur were the smallest, with females averaging 77 g and males 76 g. The average for Jodhpur is low because many immatures were trapped; however, maximum body weights recorded were not notable. Rats from Faisalabad and Rawalpindi were larger, but not necessarily older, than rats from Jodhpur.

Males from Rawalpindi showed little seasonal change in testis weights and were fertile

in all months. Sexually active males were seen in all months in Jodhpur, but the proportion of fertile males dropped to low levels in April, July, and September. No data on seasonal fertility in males rats were reported from Faisalabad.

Pregnant females occurred in every month in Rawalpindi and Jodhpur. In Faisalabad, pregnant rats were not seen in November or December. The frequency of pregnancy and ovarian weights varied seasonally in Jodhpur; it was lowest in June and October and highest in July and December. The annual frequency of pregnancy was highest in Faisalabad (46 %), next highest in Rawalpindi (39.8 %), and lowest in Jodhpur (25.5 %).

The comparative litter sizes were similar. In Jodhpur, Faisalabad, and Rawalpindi, they ranged from 6.60 to 6.19. These crude litter sizes, however, are not adjusted to account for the number of embryos actually seen at birth. Often, litter size decreases as pregnancy progresses. Counts taken in the last trimester of visible pregnancy approximate the numbers seen at birth.

We calculated the "embryo rate per 100 of all females" and from this derived the "reproductive rate" (Harrison 1952); this is the number of embryos per 100 head of population (Tab. 7). This rate is highest in rats from Faisalabad and Rawalpindi. This reproductive rate in stable rat populations is sometimes interpreted as a measure of the death rate, since births should equal deaths to maintain stability. However, high mortality in weanlings and juveniles can invalidate this assumption. In that case, the entry of young breeders (recruitment) into the population should be a better measure of the death rate.

Table 7. **Comparative reproductive data and calculated parameters for *R. rattus* from several Asian urban localities**

City	Sex ratio[a]	Crude pregnancy rate	Unadjusted embryo number	Embryo rate[b]	Reproduction rate[c]
Jodhpur	121	25.5	6.60	168	92
Rawalpindi	100	35.2	6.60	232	116
Faisalabad	117	36.1	6.19	223	120

[a] Females/100 males. – [b] Number of embryos for all females in population regardless of size. – [c] Number of embryos for 100 head of population, males and females.

The percentage of immature rats in the several populations was 13 % in Rawalpindi, 31 % in Faisalabad, and 54 % in Jodhpur. We assume that roof rat mortality (in adults) is least in Rawalpindi and greatest in Jodhpur. The reasons for the high recruitment of young rats in Jodhpur are not given by the authors, but may be due, in part, to a relatively harsh environment. In Rawalpindi, the main cause of rat mortality is year-round intraspecific strife.

Despite a high reproductive rate in Rawalpindi roof rats, the low proportion of immatures entering the population indicates high mortality among nestling and weanling rats. This could be due to desertion of litters before weaning (few lactating females were seen) or predation by adult rats.

The differing population strategies are exemplified by the Rawalpindi and Jodhpur rat populations. Whereas Rawalpindi relies upon a high reproductive rate to offset high mortality in immatures to maintain the population. Jodhpur rats rely upon a high recruitment of immatures into the population to offset the apparent high mortality in adult rats. Pregnancies at Jodhpur remain at a rather lower level than at either Rawalpindi or Faisalabad.

The implications for management of Rawalpindi rat populations are not promising. Since juvenile mortality is already high, efforts to increase adult mortality with poisons

would tend to decrease the pressure on the juveniles. The birth rate would be adjusted by the rats following population reduction to compensate for mortality, and both frequence of pregnancy and litter size would be expected to increase.

More effective control measures would be those that change the environment. Rat-proofing of grain shops, though difficult, would bring about population decreases. There are numerous holes in walls between adjoining shops that could be filled to stop rat movements. Grain shop sanitation is another measure that would be beneficial. This includes keeping grain spillage swept up and damaged bags repaired. If these measures were instituted along with poisoning and trapping, then population control would become evident – but it would have to be a continuous effort.

Acknowledgements

We appreciate the help Mohammad Ilyas, Yousaf Khan and Mohammad Nawaz provided in capturing the rats and assisting in the necropsies. We thank Liaqat Ali for entering all the necropsy and morphometric data into the dBASE III computer program. Richard A. Dolbeer and Donald J. Elias, Denver Wildlife Research Center, critically reviewed the manuscript and provided helpful suggestions.

This study was supported with funds provided by the U. S. Agency for International Development under the project "Food Security Management, Vertebrate Pest Control, PASA IPK-0491-P-IF-5017-05". We also thank the Pakistan Agricultural Research Council and the National Agricultural Research Centre, Islamabad, for providing office and laboratory space for the project.

Zusammenfassung

Reproduktionsbiologie und Populationsstruktur von Rattus rattus in Rawalpindi, Pakistan

Die Fortpflanzungsbiologie und Populationsstruktur von *Rattus rattus* wurden in einem Großhandelsmarkt für Getreide und andere Gebrauchsgüter in Rawalpindi, Pakistan, untersucht. Innerhalb von 14 Monaten wurden die Ratten in monatlichen Abständen auf dem Getreidemarkt gefangen. Wir sezierten und untersuchten insgesamt 2327 Ratten, 1175 männliche und 1152 weibliche. Es wurde festgestellt, daß die männlichen Ratten jeden Monat reproduktionsfähig waren ohne bedeutsame, saisonbedingte Unterschiede; weibliche Ratten waren jeden Monat trächtig, und die Trächtigkeitsfrequenz betrug durchschnittlich 39,8 %. Die jeweilige Embryonenzahl während des letzten Viertels der Trächtigkeit betrug durchschnittlich 6,1 ± 1,7 (SD). Auf der Basis unserer Studie von Ratten, die zum ersten Mal trugen, und von Ratten, die schon vorher trächtig waren, kalkulierten wir, daß eine geschlechtsreife weibliche Ratte im Durchschnitt 1,8 Trächtigkeiten hat. Die durchschnittliche Produktion von jungen Ratten war 10,9 pro Weibchen (6.1 × 1.8). Unreife Tiere (unabhängig, aber nicht sexuell reif) dagegen machten 13,1 % der Gesamtstichprobe aus. Nachwuchs war fortlaufend während der Studie vorhanden und wies darauf hin, daß beträchtliche Todesfälle bei Nestlingen und sexuell unreifen Tieren vorkamen. Viele Wunden und Narben an erwachsenen Tieren beider Geschlechter wiesen darauf hin, daß ein hohes Maß von Streit und Aggression zwischen den gesellig lebenden Ratten herrschte.

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Authors' addresses: JOE BROOKS, USDA/APHIS/ADC/Denver Wildlife Research Center, P. O. Box 25266, Denver, Colorado 80225-0266, USA; EJAZ AHMAD, Department of Fishery and Wildlife Biology, Colorado State University, 135 Wagar Building, Fort Collins, Colorado 80523, USA; and IFTIKHAR HUSSAIN, Vertebrate Pest Control Laboratory, National Agricultural Research Centre, Park Road, Islamabad, Pakistan

Z. Säugetierkunde 59 (1994) 218–223
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ISSN 0044-3468

Dispersal and other inter-group movements in badgers, *Meles meles*

By S. F. Christian

School of Biological Sciences, University of Sussex, Brighton, UK

Receipt of Ms. 3. 12. 1993
Acceptance of Ms. 24. 3. 1994

Abstract

Investigated dispersal and other movements of badgers between social groups in a high density badger population in Sussex, southern England, during the period November 1988 to October 1993. Fourteen badgers (10 female, 4 male) were radio-collared, tracked and observed during nocturnal ranging. Daily sleeping locations of collared badgers were also recorded for a 2-year period. In addition bait-marking was carried out twice annually to determine territory boundaries. Twenty-eight movements between groups were recorded, including 7 permanent group changes, one temporary group change and 20 visits of shorter duration. All of the adult badgers that permanently changed groups were mature females. An adult male changed groups temporarily and another was killed 3.5 km from where he was trapped. No aggression from territorial residents towards immigrants was observed and 3 females bred successfully following their group change.

Introduction

Badgers are unusual among the mustelids in that they typically live in mixed-sex social groups, sharing a communal range and one or more setts (Kruuk 1978; Powell 1979; Christian 1993). The social groups scent-mark and actively defend territories that are usually contiguous, mutually-exclusive and remarkably stable over time (Kruuk 1978; Kruuk and Parish 1982). Kruuk (1978, 1989) reportet that badgers are highly aggressive towards their neighbours and Neal (1986 p. 151) stated that 'a resident boar will fight any intruder which hasn't the correct communal scent of his social group'. Serious territorial fights have been reported (Kruuk 1978; Neal 1986; Christian 1993) and intraspecific aggression is thought to be a significant cause of badger mortality (Gallagher and Nelson 1977; Anderson and Trewhella 1985). Thus, there is a high cost to leaving the group territory and, in populations where the social structure is stable, evidence from live-trapping suggests that dispersal of juveniles from their natal group is rare (Kruuk and Parish 1982; Cheeseman et al. 1987, 1988; Evans et al. 1989). However, little has been reported about the movements of individual badgers between social groups.

The aim of this study is to report observations of social group changes and other intergroup movements by radio-collared individuals in a high-density rural population of badgers with a stable territorial structure.

Material and methods

The observations were made as part of a long-term, intensive radio-tracking study of badger behaviour and ecology in Sussex, southern England over the period November 1988–October 1993. The estimated population density was 16.7 adults per km^2 (for further details see Christian 1993). A total of 14 badgers (4 males, 10 females) from six adjacent social groups were radio-collared, tracked and observed during the night for an average of 6 hrs per badger per night during the period 1988 to 1992. Over the period October 1989 to October 1991 the setts used by radio-collared badgers as underground sleeping locations were also recorded daily. In addition, bait-marking (Kruuk 1978) was

carried out twice each year in April and November, and the results were used to determine the boundaries of the 16 group territories in the study area.

Four categories of movement between social groups were distinguished:

1. Nocturnal visits. These included brief visits to the main setts of other social groups during nocturnal ranging. They lasted from a few minutes to one hour, during which the visitor might investigate the sett from the outside, or enter it and remain underground for some time.
2. Diurnal visits. These were visits in which individuals slept for a day or two in another social group's main sett but subsequently returned to their own territory.
3. Temporary group changes. These were longer-term movements in which badgers moved from their original social group to a new one, but returned to their original group after a period of several months.
4. Permanent group changes. These were movements in which the badgers moved from their original social group to a new social group, where they remained for the rest of the study period.

Results

Permanent and temporary group changes

Twenty-eight movements between social groups were observed during the study period: eight were classed as Permanent and Temporary group changes and 20 as other movements. Seven individuals made Permanent group changes and one individual made a Temporary group change (Fig. 1). All of the six adult badgers that changed groups permanently were mature females in their second year or older and two of them were known to have bred successfully prior to moving. The seventh badger to change social groups permanently was a young cub which accompanied its mother to her new territory. The badger which made a temporary group change was an adult male that moved to a neighbouring territory for a 3-month period.

All of these badgers were in good general body condition, showed no signs of injury or ill health and were not observed to be socially peripheral or subject to persecution in their original groups. In each case of Permanent group change the social group that was joined was well-established and contained several adults of either sex, occupying a stable, well-defined territory. Two of the groups to which females moved contained at least two resident females which were known to have bred successfully in the year preceding the movement and went on to raise cubs in the year following the movement. Three of the six females that moved permanently bred successfully in their new social group within a year of moving.

In no case was aggression from residents towards immigrants or from immigrants towards residents observed. No injuries caused by intra-specific fighting were re-

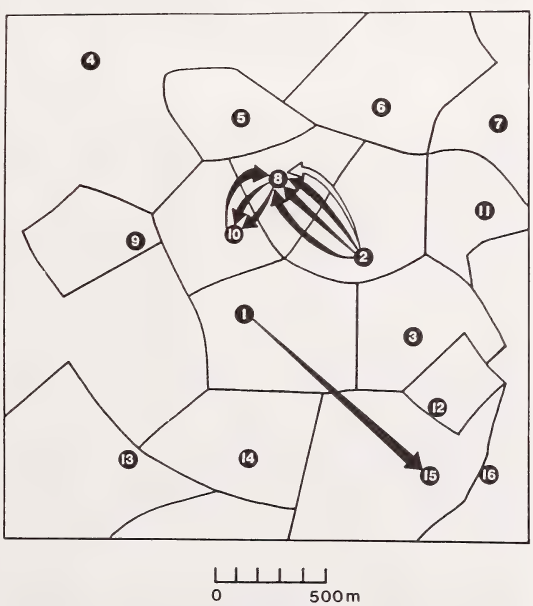

Fig. 1. Permanent (black arrows) and Temporary group changes (white arrows) by badgers, 1988–1993. Bold lines denote territory boundaries and dots numbered 1–16 denote main setts

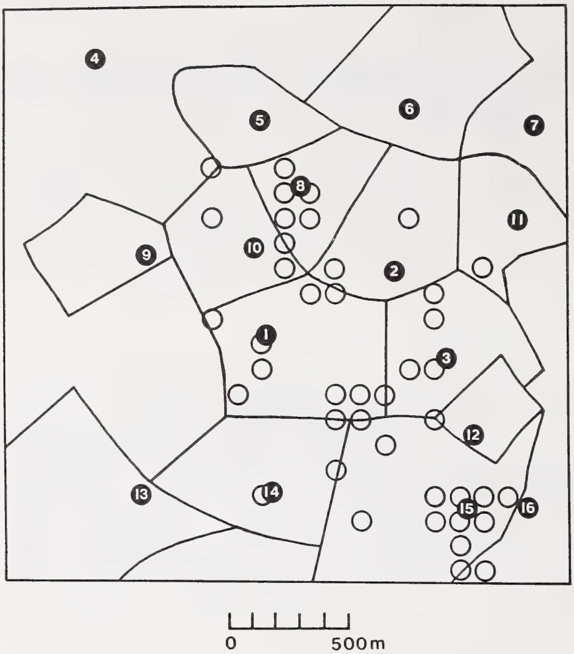

Fig. 2. Home range of female 15F1, during November 1988–October 1990. The study area was divided into 1-ha grid squares (not shown), and open circles denote squares in which 15F1 foraged. Bold lines denote territory boundaries and dots numbered 1–16 denote main setts

corded during tracking or recapture on any of the individuals that changed groups and there was no evidence of the immigrants avoiding the residents at the new sett or during nocturnal ranging.

The movement of the Group 2 badgers to Group 8 was immediate and unexpected: the badgers concerned (two females, one accompanied by a cub, and an adult male) began foraging near to a neighbouring main sett one night and by the following day had taken up residence there. In all other cases the movement from one territory to another was a more gradual process, the badgers concerned moving into outlying setts in their own territories, from these into outlying setts in the new territory and only then into the new main sett.

One case of a permanent group change is worth reporting in more detail because the badger concerned was exceptional in the extent to which it ranged within other groups' territory. The badger in question (an adult female) was trapped and collared at the main sett of Territory 1 in November 1988, and continued to inhabit that sett until February 1989, when she began to spend her days in outlying setts near the territory boundary. In early March 1989 she was found during the day at the main sett in Territory 15, and thereafter she continued to sleep at that sett (over 1.5 km from her original sett). On the night following her move, during a 5-h period, she made an extensive tour of the study area, moving through 10 different territories, passing close to the residents of several of them, and entering four main setts (Setts 1, 3, 8, and 10). Similar excursions were seen on subsequent nights and until October 1990 she was frequently located (often accompanied by a cub) foraging in other territories: particularly Territory 1 (her original territory) whose outliers she sometimes entered during the night and with whose residents she frequently associated; Territory 3 where she was recaptured in March 1990 during a nocturnal visit; and Territory 10 where she foraged with members of Groups 1 and 10 (Fig. 2). Despite this extensive extra-territorial ranging she was never observed in aggressive interactions with members of other social groups.

Other movements between social groups

Two individuals (a male and a female) made Diurnal visits to other main setts on four occasions, in January, July, August and September respectively, on each occasion spending the day underground with the residents. Fifteen Nocturnal visits (10 by females, 5 by males) were also recorded (Fig. 3). These usually lasted 5–20 minutes, during which time

the visitor sniffed around the sett entrances and sometimes entered the sett. On one occasion a female spent an hour underground at a neighbouring sett with several of its residents, having previously spent more than two hours peacefully feeding with them in a nearby maize-patch. On two occasions a male visiting a neighbouring sett was fought by an occupant and chased away, and on two occasions a male visiting a neighbouring sett was observed to copulate with a resident female.

Finally one other badger was known to have moved a long way outside of its original territory. An adult male badger was captured whilst at Sett 6 in April 1993 but was never recorded in the study area again. In October 1993 he was found dead at the side of a road 3.5 km from Sett 6.

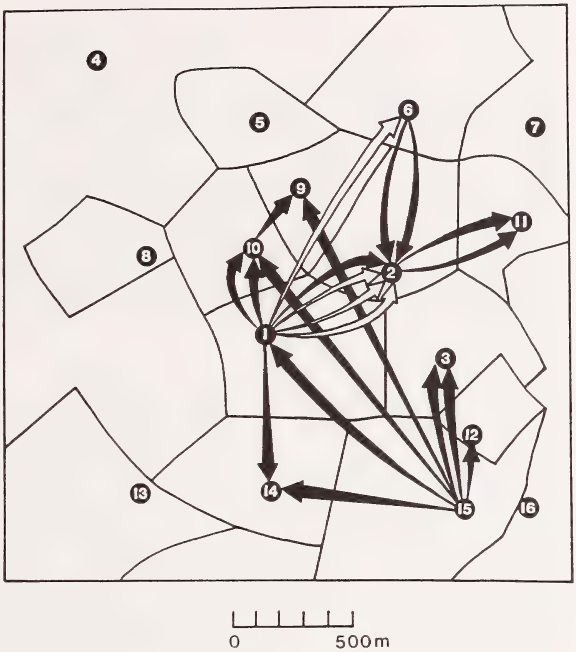

Fig. 3. Nocturnal (black arrows) and Diurnal visits (white arrows) by badgers, 1988–1993. Bold lines denote territory boundaries and dots numbered 1–16 denote main setts

Discussion

Several studies suggest that the movement of adult badgers between groups is rare. Kruuk (1978) reported that movements between territories in Wytham Woods were infrequent and in Speyside (Kruuk 1989) he found that of 60 badgers caught in consecutive years (37 females, 23 males) only six (all male, all adult) emigrated from their original territories. He concluded that male badgers remain in their natal territories for as long as it takes to move to a vacancy in a neighbouring territory, or until evicted by a relative or a usurper, whereas females remain permanently in their natal territories.

In other populations, however, both sexes may change social groups. Cheeseman et al. (1988) reported dispersal and movement patterns in badger populations in rural Gloucestershire and suburban Bristol. In the lower-density Bristol population the social structure appeared to be fluid and inter-group movements were relatively common. Movements were less frequent in the high-density Gloucestershire population, although their incidence increased as a result of disturbance, involving the complete removal of 11 social groups for reasons of disease control. In both populations, more males than females changed groups. Most of these movements involved sexually mature individuals and constituted movements to neighbouring territories. In a low-density rural Irish population subject to frequent human persecution, Sleeman (1992) reported that long-distance movements between social groups by individuals of both sexes may be relatively common. Similarly, Roper and Lüps (1993) have reported an increase in extra-territorial ranging and nocturnal visits to a main sett following the sudden death of all of its male occupants. Thus, overall the evidence points to the idea that in undisturbed high-density rural populations, where all

the available habitat is divided up in a well-defined and stable territorial system, movements from one social group to another are uncommon and largely involve the occasional movement of individuals, usually males, to neighbouring social groups. In areas where the removal of social groups, persecution or some other factor causes territorial disruption, or severely depresses the population, extra-territorial movements and group changes are probably much more frequent.

My results are consistent with these findings in two respects, in that all of the movements involved adults (with the exception of an accompanying cub) and all of the permanent group changes involved movement to an adjacent territory. However, the observed movements were relatively frequent (7 of 14 radio-collared badgers changed groups during a 3-year period and visits to other setts were relatively common) and permanent group changes exclusively involved mature females. Females also visited other main setts more frequently than males.

My observations of group changes are notable in several other respects. Firstly, dispersers were never observed suffering aggression from members of their own social group prior to changing social groups. This suggests that the individuals did not disperse because they were induced to do so by other group members. Secondly, dispersers were never observed fighting with members of their new social group. Female immigrants showed no signs of persecution but went on to breed simultaneously with resident females in the new social group. This suggests that badgers may be more free to move social groups than previously thought and suggests females may not be in direct competition with each other for opportunities to breed as has been reported in other populations (Kruuk 1989; Woodroffe and Macdonald 1993). Thirdly, the unchallenged movements through other territories suggest that under certain circumstances some individuals, or categories of individual, may be free to range and forage within other territories and to visit other setts. Finally, the movement of all of the known members of Group 2 to join Group 8 "en masse" (2 adult females, a dependent cub and an adult male) is the first reported group movement of its kind. It is important to note that the Group 2 badgers did not move to a previously unoccupied territory, nor did they take over a previously occupied territory and expel its occupants. Rather, the immigrants joined the existing group members in their main sett, associating frequently and harmoniously with them, and both immigrant and resident females went on to successfully rear cubs following the group change.

Visits to other setts by radio-collared badgers of both sexes were relatively common and were characterised by amicable association between visitors and residents. Visitors sometimes entered the new sett and even spent the next day underground there with residents. Visiting males twice achieved successful matings with resident females. On two other occasions, however, male visitors were attacked and chased away by a resident male.

These radio-tracking observations indicate that, even within a stable and undisturbed high-density rural population, interaction and movements between neighbouring social groups may be more common than has previously been estimated on the basis of recaptures at main setts. They also suggest that territoriality may be more flexible (seasonal or context-related), or more specific (only concerning specific individuals or categories of individual, e.g. adult males) than has been previously supposed.

Acknowledgements

I would like to thank David Fee for his company and assistance with fieldwork. I am also grateful to Tim Roper for allowing me to use his unpublished observations and for helpful comments on drafts of this manuscript. My research was supported by an SERC studentship.

Zusammenfassung

Ausbreitung und andere Ortsbewegungen zwischen Gruppen von Dachsen, Meles meles

Untersucht wurden Ausbreitung und andere Ortsbewegungen zwischen sozialen Gruppen einer Dachs-Population mit hoher Dichte in Sussex, Südengland, von November 1988 bis Oktober 1993. Vierzehn Dachse (10 weiblich, 4 männlich) wurden mit Radio-Transmittern markiert und während ihrer nächtlichen Wanderungen verfolgt und beobachtet. Über einen Zeitraum von 2 Jahren wurden die Schlafplätze täglich registriert. Außerdem wurde zur Feststellung der Territoriengrenzen zweimal im Jahr das Futter mit farbigen Plastikquadern markiert. Es wurden 28 Bewegungen zwischen Gruppen beobachtet, darunter 7 dauerhafte Gruppenwechsel, ein vorübergehender Wechsel und 20 von kürzerer Dauer. Alle adulten Dachse, die dauerhaft die Gruppe wechselten, waren geschlechtsreife Weibchen. Ein adulter männlicher Dachs wechselte die Gruppe nur vorübergehend, ein anderer wurde 3,5 km von der Fangstelle entfernt getötet. Territorienbesitzer zeigten keine Aggression gegenüber Einwanderern. Drei weibliche Dachse zogen nach Gruppenwechsel erfolgreich Nachwuchs auf.

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Author's address: S. F. Christian, School of Biological Sciences, University of Sussex, Brighton BN1 9QG, UK

Z. Säugetierkunde 59 (1994) 224–229

ISSN 0044-3468

Lipid deposits in pregnant and non-pregnant bats (*Pipistrellus pipistrellus*)

By Pilar López-Luna, F. Arevalo, M. J. Burgos, and N. del Hoyo

Departamentos de Fisiología y Farmacología, Biología Animal y Bioquímica y Biología Molecular, Universidad de Alcalá, Alcalá de Henares, Madrid, Spain

Receipt of Ms. 15. 12. 1993
Acceptance of Ms. 1. 3. 1994

Abstract

Studied the white and brown adipose tissues of female bats (*Pipistrellus pipistrellus*) in order to ascertain differences in relative lipid, fatty acid and phospholipid contents that might be related to pregnancy. Relative lipids were higher in the white adipose tissue of pregnant bats than in that of non-pregnant bats, and the same was true for phospholipids in the brown adipose tissue. Pregnancy in *P. pipistrellus* could be responsible for the changes in the length and unsaturation of some fatty acids in both kinds of adipose tissue.

Introduction

Reproduction is accompanied by an increase in energy demands (Towsend and Callow 1981). The total energy investment of pregnancy involves many components such as production of fetal, uterine, placental, and mammary tissue, as well as the production and increased maintenance costs associated with the new tissues. It has been suggested that suppressing metabolic energy expenditure increases energetic efficiency during pregnancy (Schneider and Wade 1987). Although in many mammals the energy thus conserved is first stored as white adipose tissue and later mobilized to meet the energy demands of lactation (Naismith et al. 1982; Sadleir 1984), this reserve is apparently not used by small insectivorous bats (Racey and Speakman 1987). However, fat storage may be important in bats because of their unavoidably high activity levels and obvious flight costs (Gittleman and Thompson 1988).

Maternal body fat accumulation is one of the most striking features of gestation in both women (Hytten et al. 1966; Hytten and Leitch 1971) and experimental animals (Beaton et al. 1954; Lopez-Luna et al. 1986; Herrera et al. 1988). Fat storage may also be important in pregnant bats since, when fat is unavailable, fetal growth rates and pregnancy rates often decline (Racey 1973; Kurta 1986).

The main purpose of this study is to learn whether pregnant females of *Pipistrellus pipistrellus* show differences in body weight, total lipids, fatty acids and phospholipids in the white and brown adipose tissues compared with non-pregnant female individuals.

Material and methods

Animals

The active bats used in this study were pregnant and non-pregnant *Pipistrellus pipistrellus* females captured alive in eastern Madrid, between June 28 and July 31 and between March and September, respectively. The pregnant bats were gathered from their maternity roosts (an inhabited building) between 19:00 and 22:00 h.

Bats were placed in a wet sack for transportation to the laboratory and weighed and killed by exsanguination under diethyl ether anaesthesia 2–3 hours after collection. The abdomen was immediately opened and conceptus (fetus and placenta) were delivered by hysterectomy and weighed.

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The subcutaneous white and interscapular brown adipose tissues were quickly removed, stripped of connective tissue, excised, weighed and immediately frozen in liquid nitrogen. They were then kept frozen at –30 °C until lipid analysis. Standard fatty acids were purchased from Carlo Erba (Milan, Italy) and Alltech Associates (Deerfield, IL, USA).

Lipid analysis

Lipids were extracted from frozen tissues and purified with chloroform:methanol (2:1), according to the method of FOLCH et al. (1957). After evaporation of the solvent, the lipids were stored in a N_2 atmosphere at –30 °C.

The method of ROUSER et al. (1966) was used for quantitative determinations of total phospholipid from both tissues. Purified total lipids from both tissues were directly treated with BF_3/CH_3OH to obtain the fatty acid methyl esters as previously described by PULIDO et al. (1986). A Pye Unicamp Philips gas chromatograph equipped with a flame ionization detector was used to assay the products in a 5 m × 2 mm glass column packed with 20 % Silar 10 C on 80/100 Chromosorb WHP (Alltech Associates); the flow rate of the nitrogen carrier gas was 32 ml/min.

Statistical treatment of the results

Absolute and relative values are expressed as mean ± SE. The statistical significance of differences between groups was determined by Student's t-test and differences were considered significant when $p < 0.05$.

Consent for capturing the animals was given by the Consejeria de Medio Ambiente (Comunidad de Madrid) in accordance with the Bern Agreement (1979) ratified by the Spanish Government in 1986.

Results

As shown in table 1 the conceptus-free body weight of pregnant bats was significantly higher ($p < 0.05$) than the body weight of non-pregnant bats. The pregnant bats studied had each one fetus which weighed between 0.76 and 1.12 g. However, the subcutaneous

Table 1. **Absolute body weights and relative tissue weights, relative lipid content and relative phospholipids in white and brown adipose tissues in non-pregnant and pregnant females of *P. pipistrellus***

The results are given as mean ± SE. Comparisons of pregnant vs non-pregnant

	Non-pregnant (n = 28)	pregnant (n = 15)
Body weight (g)	3.9 ± 0.04	4.2 ± 0.1*
White adipose tissue		
weight (mg wet tissue/g body wt)	32.9 ± 2.4	28.6 ± 5.4
lipids (g lipid/g wet tissue)	0.19 ± 0.02	0.32 ± 0.06**
Phospholipids (µmol/g wet tissue)	2.2 ± 0.2	2.5 ± 0.6
Brown adipose tissue		
weight (mg wet tissue/g body wt)	10.9 ± 0.6	12.0 ± 0.8
lipids (g lipid/g wet tissue)	0.26 ± 0.02	0.27 ± 0.02
Phospholipids (µmol/g wet tissue)	18.9 ± 1.9	27.5 ± 4.7***

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

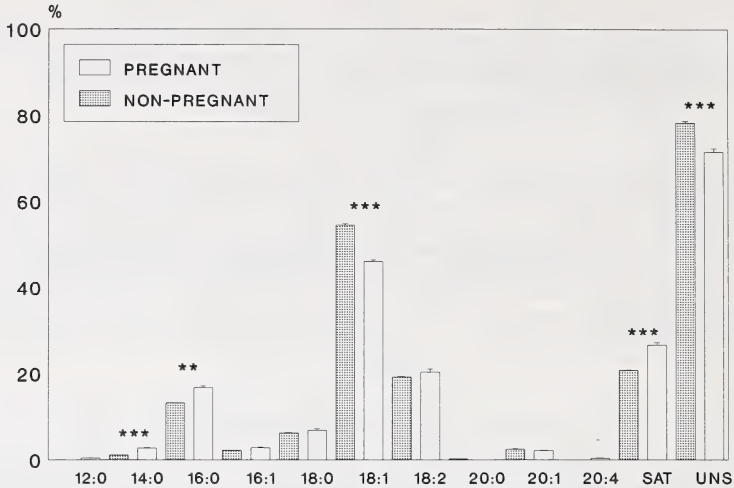

Fig. 1. Fatty acid composition of subcutaneous white adipose tissue in *P. pipistrellus.* All assays were performed in duplicate. The values given as % total fatty acids are means ± SE. Asterisks show statistical comparisons between pregnant and non-pregnant bats $^{**}p < 0.01$, $^{***}p < 0.001$

white adipose tissue (WAT) weight relative to body weight does not show significant differences between pregnant and non-pregnant animals. The relative lipid content (g. lipid/g wet tissue) was higher in pregnant than in non-pregnant bats ($p < 0.01$). Interscapular brown adipose tissue (BAT) weight and relative lipid content was not modified during pregnancy. Relative phospholipids from WAT were unmodified during pregnancy although BAT relative phospholipids increased significantly ($p < 0.001$) during pregnancy (Tab. 1).

Distribution of fatty acids in the total lipids from WAT tissue for non-pregnant and pregnant bats is shown in figure 1. The proportion of myristic acid (14:0) and palmitic acid (16:0) in the WAT of pregnant bats is higher ($p < 0.001$ and $p < 0.01$ respectively) than that observed in non-pregnant bats. However, lauryl acid (12:0) was only present in WAT from pregnant bats and arachidonic acid (20:4) only appeared in non-pregnant bats.

Pregnancy did not significantly affect the percentages of unsaturated fatty acid in WAT, with the exception of oleic acid (18:1), which decreased ($p < 0.001$) in pregnant bats.

The fatty acid in total lipids of BAT (Fig. 2) shows an increase in oleic acid (18:1) monounsaturated fatty acid and a decrease in linoleic acid (18:2) polyunsaturated fatty acid that were both statistically significant ($p < 0.001$). The fatty acid composition of the total lipids in WAT and BAT (Figs. 1, 2) shows few differences between pregnant and non-pregnant bats. Unsaturated fatty acids are the most abundant (71–78 %) in both kinds of tissues and in both pregnant and non-pregnant bats. However, the level of saturated fatty acids increased during pregnancy from 21 to 27 % ($p < 0.001$) in WAT, but not in BAT, where the level remained constant (21 %).

Discussion

Although copulation by temperate-zone insectivorous bats normally occurs in autumn, fertilization does not occur until early spring when the bats arouse from hibernation and enter maternity colonies (Racey 1982). The length of gestation in heterothermic bats may

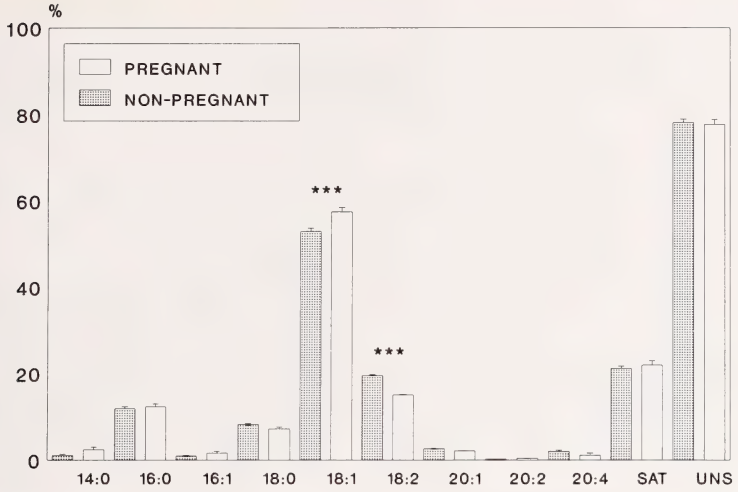

Fig. 2. Fatty acid composition of interscapular brown adipose tissue in *P. pipistrellus.* The same symbols as in figure 1 were used

vary with the external conditions of food supply and temperature. The pregnant *P. pipistrellus* bats studied here carried only one pup, and, according to date of capture (last week of June or first of July), size of the fetuses, and the results reported by Racey and Swift (1981), gestation was probably far advanced.

The increase of body weight in these *P. pipistrellus* at late gestation is not due only to the presence of the conceptus since the excess weight persists after calculating the conceptus free maternal body weight. Such weight increase in gestating females has also been observed in other bat species (Stebbings 1976; Studier and O'Farrell 1976; Speakman and Racey 1987). The mass increase in *P. pipistrellus* is partially explained by the enlargement of the mammary glands.

In our study the weight of subcutaneous WAT in pregnant bats showed no significant difference compared with that in non-pregnant individuals. However, although increased fat during pregnancy has been detected in *M. lucifugus, P. auritus* (Speakman and Racey 1987) and *M. grisescens* (Krulin and Sealander 1972), it cannot be completely confirmed since Studier and O'Farrell (1976) found no evidence of fat increase during pregnancy in *M. lucifugus* and *M. thysanodes.*

Our results for WAT weight and lipid content suggest that *P. pipistrellus* responds to the increased energy requirements of pregnancy by increasing the caloric content of the fat rather than by increasing the amount of fat stores, as Pistole (1989) has also suggested in pregnant *Eptesicus fuscus.*

The main alteration in the pattern of total lipid fatty acid composition in WAT of *P. pipistrellus* caused by pregnancy could indicate increased lipogenesis in this tissue during gestation as also occurs in pregnant rats (Palacin et al. 1991).

Brown adipose tissue, traditionally associated with thermogenesis, plays an important role in maintaining the energy balance in small mammals (Rothwell and Stock 1983; Himms-Hagen 1983; Trayhurn 1984). It has been previously shown that there is an increase of BAT during late pregnancy in the rat (Agius and Williamson 1980; Lopez Luna et al. 1991). The present results show that BAT tissue weight and total lipids remain unmodified in *P. pipistrellus* during pregnancy.

Similarly, the fatty acid profile of BAT from pregnant bats was similar to non-pregnant ones; however the levels of the 18:2 and 20:4 fatty acids were decreased, which could be

related to their importance in the prostaglandin production involved in the normal parturition process (Arahuetes et al. 1982).

Although BAT wheight, lipid content, and fatty acid do not differ between pregnant and non-pregnant bats, the phospholipid levels are higher in pregnant than in non-pregnant bats. The scarce bibliography does not help explaining the rise we found in BAT phospholipids from pregnant bats.

Cold and diet have also been reported to modify BAT phospholipid composition and/or content (Giradier 1983; Ide and Sugano 1988; Arévalo et al. 1990). Masoro (1968) suggests that muscle phospholipids may serve as an energy source, but we cannot affirm whether the phospholipids of brown fat are an energy source or not.

Several factors, like quantity and nature of food, temperature, or physiological state, are known to affect the fat composition of mammals (Pearce 1983). Present findings show that in *P. pipistrellus* gestation may produce changes in the length and/or unsaturation of some of the fatty acid chains as well as in their fat composition. In this sense Lockwood et al. (1970) have shown that sex hormones are involved in controlling the specific activities of lipogenic enzymes in both male and female rats. In fact, and as Pistole (1989) suggests, bats alter their fat composition in response to a particular energy need such as hibernation, pregnancy or lactation.

Acknowledgements

We wish to thank Dr. Pérez-Suarez for his field assistance and Carol F. Warren of the translation service at the Instituto de Ciencias de la Educación (ICE) of the University of Alcalá de Henares. This investigation was supported in part by the Comisión Asesora de Investigación Científica y Técnica, Project: PB85--0242, Spain.

Zusammenfassung

Fettspeicher in trächtigen und nicht trächtigen Fledermäusen (Pipistrellus pipistrellus)

Weißes und braunes Fettgewebe von graviden und nicht graviden Fledermaus-Weibchen (*Pipistrellus pipistrellus*) wurde analysiert, um trächtigkeitsbedingte Änderungen im Gesamtgehalt von Lipiden, Fettsäuren und Phospholipiden festzustellen. Der Gesamtanteil an Lipiden war in weißem Fettgewebe bei trächtigen höher als bei nicht trächtigen Fledermäusen. Das gleiche traf für die Phospholipide im braunen Fettgewebe zu. Die Trächtigkeit bewirkt bei *P. pipistrellus* in beiden Typen von Fettgeweben Änderungen in der Länge der Fettsäuren und deren Anteil an ungesättigten Bindungen.

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Authors' addresses: Prof. P. López Luna, Departamento de Fisiología y Farmacología; Dr. F. Arévalo, Departamento de Biología Animal; Dr. N. del Hoyo, Departamento de Bioquímica y Biología Molecular; M. J. Burgos, Departamento de Fisiología y Farmacología, Universidad de Alcalá, E-28871 Alcalá de Henares, Madrid, Spain

Z. Säugetierkunde 59 (1994) 230–235

ISSN 0044-3468

On the suckling behaviour of Alpine chamois *Rupicapra rupicapra rupicapra*

By K. Ruckstuhl and P. Ingold

Zoology Department, University of Berne, Switzerland

Receipt of Ms. 24. 9. 1993
Acceptance of Ms. 9. 12. 1993

Abstract

The suckling behaviour of 9 mother-kid pairs of alpine chamois (*Rupicapra rupicapra rupicapra*) was studied from May to October 1991. Duration of suckling bouts decreased with age of the young, from a mean of 48 sec in the first month, to 22 sec in October, whereas the time between suckling increased from 25 min to over 160 min. Suckling success (number of successful suckling attempts over all attempts) of the young decreased from the first month up to the time when the young were weaned. Suckling was always terminated by the mother (except 2 times). After the third month of life, mothers only allowed suckling by their kids from the side. Each suckling attempt from behind was rebuffed.

Introduction

Lactation is of fundamental importance for young mammals, for growth and building up body reserves (Clutton-Brock 1982). While the young attempt to obtain as much parental care (e. g. milk) as possible, mothers are selective in maximising the difference between the benefit and cost of parental care. If they invest too much in their current offspring, it may decrease their chances of survival and the number of future offspring (especially when the females are young). This asymmetry of benefits and costs between mothers and young gives rise to a parent-offspring conflict over the amount and termination of parental investment (Trivers 1985). Studies on ungulates indicate that the young attempt to suckle as long as possible, while mothers increasingly refuse to suckle them (e. g. Berger 1979; Clutton-Brock 1982). Moreover, it could be of some importance from which position (i. e. from behind or from the side) a kid attempts to suckle.

In chamois, no detailed study is yet available describing the suckling behaviour of females and kids for the entire lactation period.

The aim of the present study was to investigate the suckling behaviour of mothers and kids over the entire suckling period: the duration and frequency of suckling bouts and the suckling success rate of the kids. Furthermore, it was of interest to determine who terminates such suckling bouts and if mother and kid agree or differ in their preference of suckling positions.

Material and methods

Study area and animals

Nine individually marked female chamois and their kids were observed on 70 days (617 hours) between May and October 1991, in the region of Augstmatthorn, Bernese Oberland, Switzerland. The study site lies within the borders of an area where hunting is prohibited. Chamois were captured in a wooden trap (with salt as bait) and individually marked with yellow-coloured plastic stripes glued around their horns. Females with their young spent most of their time on grassy slopes at an altitude between 1400 and 2137 m a.s.l. with only little tree cover, where they could be easily observed (Ingold and Marbacher 1991).

Time of birth was estimated to be mid-way between the last observation, that a female was seen without a kid and the first day when she was observed with it. Kids were not marked, but as female

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chamois only suckle their own kids (Krämer 1969), it was possible to determine which kid belonged to each marked female.

The sex of the kid was determined through the kid's position while urinating (Tab. 1).

Data on suckling behaviour were collected from an observation point where most of the slope used by the chamois during daytime was visible. Observations were made with a spotting scope (30 × 60) and binoculars (10 × 40).

Table 1. **Age of female Alpine chamois in years, sex and date of birth of young and observation time of each mother-kid pair (in days and hours visible), at the Augstmatthorn, Switzerland, 1991**

Age of female	Date of birth	Sex of kid	Days of observation	Hours
5	08.–20. May	f	9	39
5	21.–26. May	f	10	55
5	08.–20 May	m	16	79
7	20.–22. May	f	12	69
8	08.–20. May	f	13	81
8	08.–20. May	f	17	93
8	03.–12. June	f	12	61
11	08.–20. May	f	11	48
13	08.–20. May	m	15	92

Data collection

Each mother-kid pair was observed for 9 to 17 days, depending on their presence and visibility. If several marked females were visible at the beginning of data collection, the female with the least observation days or hours was chosen as focal animal. Data on suckling behaviour were collected with the focal animal-continued sampling method. Durations of suckling bouts for females that were not focal animals were collected ad libitum (Altmann 1974).

Duration of suckling bout was measured as the time from the first contact of the kid with the udder, until the kid itself or the mother terminated the suckling. Suckling bouts were timed to the nearest second.

During a suckling bout the kid was either in contact or pulled at the udder. Suckling attempts were considered successful, when they lasted more than 5 seconds. Attempts where no contact was made with the udder, or bouts where the contact was shorter than 5 seconds, were treated as unsuccessful suckling attempts. A kid's suckling attempt was rejected, when the female did not allow it to suckle or even approach the udder. Time between suckling bouts was measured in minutes from the end of the last successful suckling bout until the commencement of the next bout.

Suckling success was calculated from the number of successful suckles divided by the number of all suckling attempts.

The position of the kid relative to the mother during suckling was recorded after each suckling bout or attempt.

Statistical analysis

Mean duration of suckling bouts and time between suckling were calculated separately for each mother-kid pair for the first six months of life of the young.

Differences in duration of suckling bout and time between suckling (dependent variables) were tested with a 2-way ANOVA (Zar 1984) according to individual variation and age of the kids. Age of the kids and individual differences were treated as independent variables.

Suckling success: the mean suckling success was calculated (for each kid) for each month of life and tested with a Spearman rank correlation coefficient.

Results

The duration of suckling bout decreased with age of the young (Fig. 1; 2-way ANOVA; $F = 63.77$, $df = 1$, $p < 0.001$). Differences in suckling duration between individuals had no influence on the decrease in suckling duration over the months observed ($F = 1.01$, $df = 8$, $p = 0.44$).

Although suckling was observed occasionally in October, it did not occur in November and after the rut (4 days of observation).

The time between suckling bouts increased during the first 5 months of the kids' life (Fig. 2; 2-way ANOVA; $F = 33.24$, $df = 1$, $p < 0.001$). Individual differences had no influence on the average increase in time between suckling bouts ($F = 0.99$, $df = 8$, $p = 0.47$).

Kids either suckled from the side (their body antiparallel to their mothers') or from behind (Tab. 2). They butted the udder 3 to 5 times before holding their heads still and

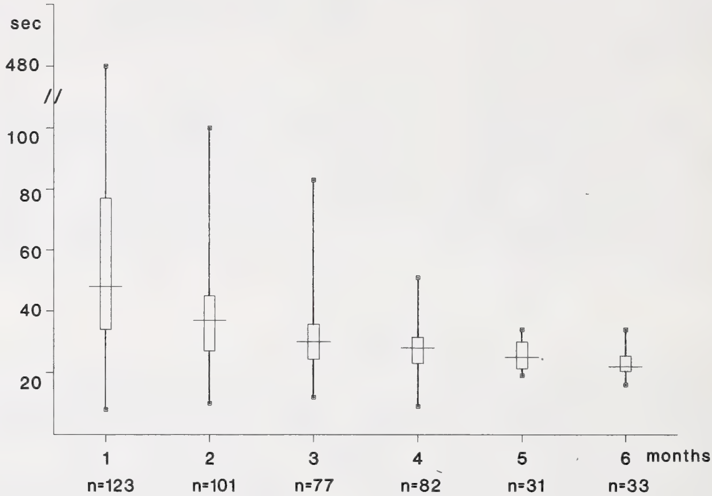

Fig. 1. Duration of suckling bouts in the first six months of life for Alpine chamois at the Augstmatthorn, Switzerland, 1991. (Mean, minima, maxima, 1st +3rd quartile). Data of 9 mother-kid pairs

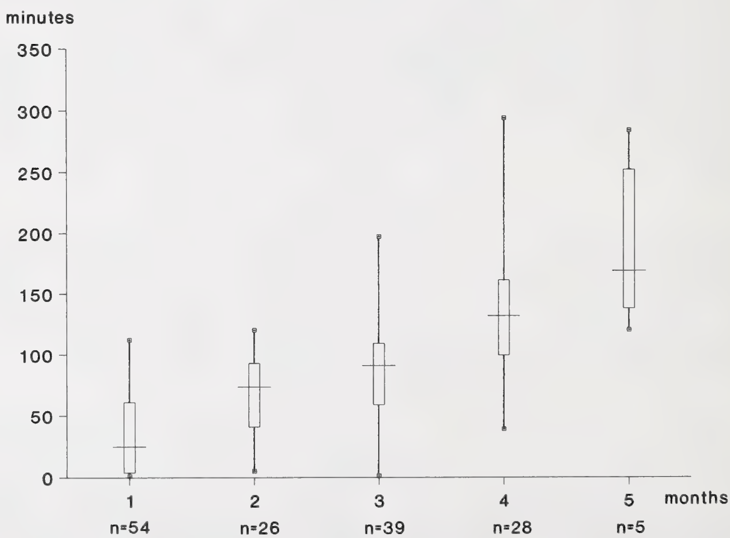

Fig. 2. Time between suckling bouts in the first 5 months of life of Alpine chamois at the Augstmatthorn, Switzerland, 1991. (Mean, minima, maxima, 1st +3rd quartile). Data of 9 mother-kid pairs

Table 2. **Number of successful or unsuccessful suckling attempts from the "side" or "from behind" position**

Data from Alpine chamois at the Augstmatthorn, Switzerland, 1991. Data of 9 mother-kid pairs

Age in months	1		2		3		4		5		6	
Position	s	b	s	b	s	b	s	b	s	b	s	b
Total attempts	163	77	69	42	92	88	91	41	28	24	31	12
% successful	71	51	79	17	68.5	2	66	0	82	0	42	0
% unsuccessful	29	49	21	83	31.5	98	34	100	18	100	58	100

b = from behind; s = from the side.

suckling. During the first months 75 % of the successful bouts were from the side. In the second and third months, 88 % and 97 % of all successful sucklings were from the side. After the third month of life, suckling attempts from behind were always rejected by the mother.

Suckling success in general decreased with the age of the kids (Fig. 3; Spearman Rank correlation coefficient; rs = 3.64 N = 40, $p < 0.05$).

Suckling was always terminated by the mother (n = 474) except in May, when 2 kids interrupted the suckling themselves (n = 2 out of 163 suckling bouts; 9 individuals were observed for a total of 40 hours).

In May, kids sometimes were observed attempting to suckle from mothers other than their own, but each of these attempts was rebuffed by the females, either by walking away or by butting the kid away.

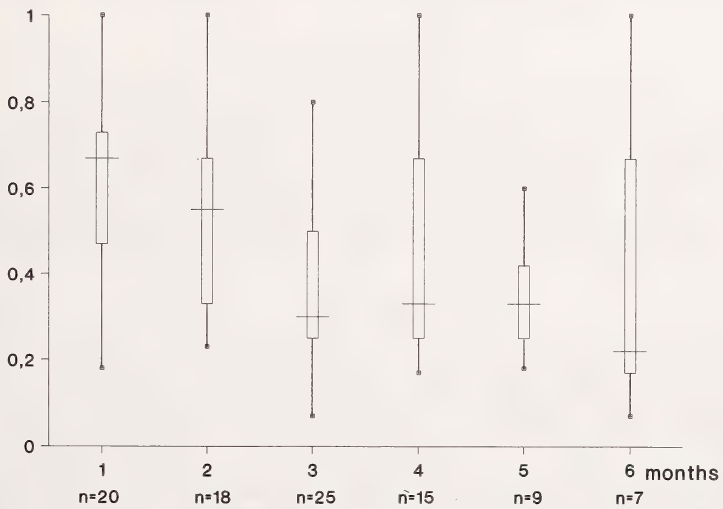

Fig. 3. Suckling success (number of successful suckling attempts over all attempts) of chamois kids during the first 6 months of life at the Augstmatthorn, Switzerland, 1991. (Mean, minima, maxima, 1st +3rd quartile), n = total number of suckling attempts. Data of 9 mother-kid pairs

Discussion

The decrease in duration of the suckling bout, frequency and success is very similar to those described in other studies on ungulates (red deer: Clutton-Brock 1982; bighorn sheep: Berger 1979; Festa-Bianchet 1988; bison: Green 1986). As the young grow older, they appear to receive less milk and are admitted to the udder less often. In spite of being rebuffed the kids try to gain access, and after the 4th month of life the total number of suckling attempts decreases. Weaning in chamois is a gradual process, with little conflict between mother and young, and aggressive behaviour by the young was never observed, as in monkeys (Gomendio 1991; Goodall 1990; Trivers 1974, 1985) towards the mother when refused to suckle. Kids simply attempt to suckle again, after being rebuffed, or wait for another opportunity. The mother decided how long and when she wanted to suckle her kid. The probability of a kid suckling successfully not only depended on the frequency and duration of suckling bouts but also on the kid's position towards the udder during suckling attempts. Approaches from the side were more successful. After the third month of life, all suckling attempts from behind were rejected by the mother. It probably was easier for the mother to keep on walking when the kid attempted to suckle from behind. When it tried to suckle from the side, the female had to lift her leg and step over her young. Perhaps the mother also had better control (visible and olfactory) over the kid who wanted to suckle, when it approached her from the side. Mother and kid therefore not only differed in their interest in the duration and frequency of suckling bouts but also in their preference of the suckling position.

Acknowledgements

We thank the Federal Game Department for supporting the study financially and the Game Department of the Canton of Berne for its cooperation and P. Neuhaus, M. Güntert and D. Seip for comments on earlier drafts of this paper.

Zusammenfassung

Zum Saugverhalten bei der Alpengemse Rupicapra rupicapra rupicapra

In einem Gebiet im Berner Oberland, Schweiz, wurde von Mai bis Oktober 1991 das Saugverhalten von Gemsen (*Rupicapra rupicapra rupicapra*) untersucht. Während die durchschnittliche Saugdauer bei den Kitzen über die Monate immer kürzer wurde, nahm die Zeit zwischen dem Saugen zu. Kitze wurden immer seltener und in größeren Abständen gesäugt. Außer zweimal im Mai wurden alle Saugakte von der Geiß abgebrochen. Saugversuche der Kitze blieben immer öfter erfolglos. Ab dem dritten Lebensmonat der Kitze lehnte die Geiß alle Saugversuche des Kitzes von hinten ab.

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Authors' address: Lic. phil. nat. K. Ruckstuhl and Prof. Dr. P. Ingold, Zoology Department, Ethology and Nature Conservation, University of Berne, Länggaßstr. 27, CH-3012 Berne, Switzerland

Z. Säugetierkunde 59 (1994) 236–245

ISSN 0044-3468

Genetic relationships of some *Gazella* species: an allozyme survey

By M. Vassart, L. Granjon, A. Greth, and F. M. Catzeflis

Ecole Nationale Vétérinaire de Toulouse, Toulouse, France; Museum National d'Histoire Naturelle, Paris, France; National Wildlife Research Center, Taif, Saudi Arabia; and Institut des Sciences de l'Evolution, Université de Montpellier II, Montpellier, France

Receipt of Ms. 22. 11. 1993
Acceptance of Ms. 17. 1. 1994

Abstract

An allozyme comparison of eight taxa in the genus *Gazella* (Bovidae: Artiodactyla) was conducted to clarify the systematic relationships of endangered gazelles currently bred in Saudi Arabia for reintroduction. Electrophoretic variation at 16 genetic loci suggested that several similar taxa of Arabian gazelles, namely *G. gazella gazella, G. gazella erlangeri, G. gazella farasani*, and *G. gazella cora*, belong to the same species of *G. gazella* sensu lato. Four other species proved to have diverged genetically: *G. thomsoni* and *G. dorcas*, which cluster together, *G. rufifrons*, and *G. subgutturosa*. The subgenus *Trachelocele*, in which the latter species has been placed according to morphological characteristics, is not supported. Polymorphism and heterozygosity values found in *Gazella* were generally similar to average values reported for mammals. The results are discussed in terms of the strategy to follow a conservation program that take genetic data into account.

Introduction

There is urgent need for conservation action concerning gazelles (Ryder 1987), both in captive and wild populations. Of the 12 species of *Gazella* (Corbet and Hill 1980), nine are considered vulnerable or endangered (IUCN 1988), mainly due to overhunting and habitat destruction. In Saudi Arabia, where at least three "good biological species" (Mayr 1963) are found: *G. saudiya, G. subgutturosa* and *G. gazella* (see Fig. 1), the situation is of particular concern (Thouless et al. 1991). Over the last few years, tremendous efforts have been undertaken towards the conservation of gazelles in this country (Abu-Zinada et al. 1989). It is widely accepted that species conservation must be based on proper systematics of the endangered taxa (Ryder 1986; Groves 1988).

Morphological characters such as size and shape of horns and skull have been previously used to establish systematics in *Gazella* (Groves 1969, 1983; Lange 1972; Groves and Lay 1985; Alados 1986/1987). Color and coat patterns have also been used, but these characters may vary due to environmental conditions (Harrison and Bates 1991; Groves and Lay 1985). Cytotaxonomy seems to be particularly informative, and can be helpful in characterizing some species, as the Indian-gazelle, *G. bennetti* (Furley et al. 1988). Up to now, only limited data on the genetic diversity in the genus *Gazella* are available based on protein electrophoresis (Templeton et al. 1987; Granjon et al. 1991). This technique has proven to be useful in a number of studies both for captive breeding management purposes (see Wayne et al. 1986) and for systematic and phylogenetic studies (see Buth 1984 for a review). Advocating a phylogenetic basis for taxonomy, including subspecies groupings (see Cracraft 1989 for a discussion of the phylogenetic species concept), the present study shows the results of allozyme variation in eight taxa of gazelles and proposes some hypotheses on the phylogeny and conservation of this group.

In particular the following questions were posed: 1. Among the three species present in

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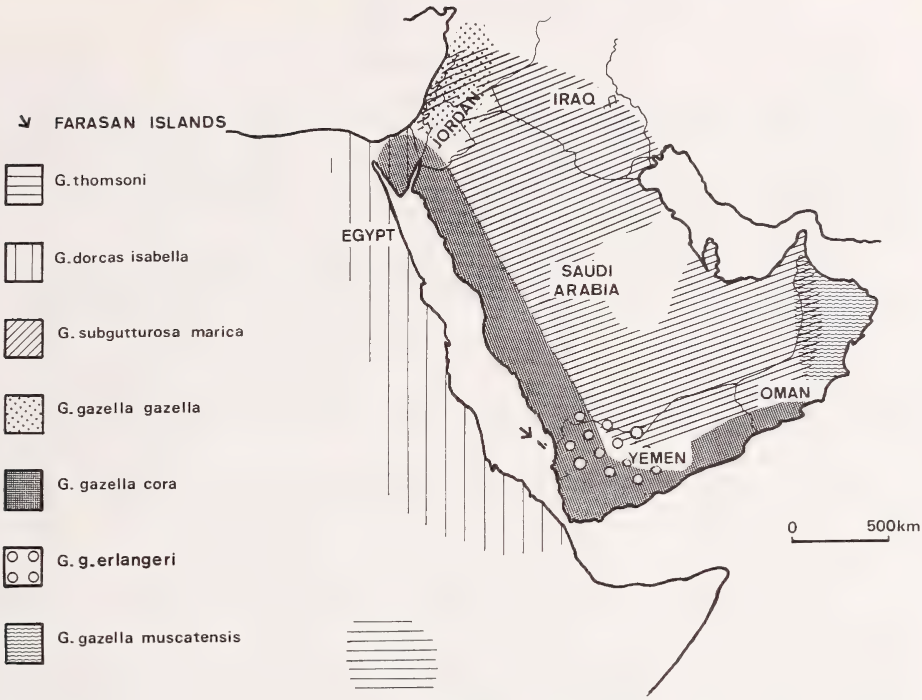

Fig. 1. Distribution of eight taxa of *Gazella* in the Arabian peninsula and in East Africa. On Farasan Islands lives *G. g. farasani.* Areas of sympatry for *G. g. gazella* and *G. g. cora, G. g. cora* and *G. g. erlangeri* are temptative. Data from Groves (1985), Dorst and Dandelot (1972), Harrison and Bates (1991) and Kingswood and Kumamoto (1988)

Saudi Arabia, *G. subgutturosa* has been considered very divergent morphologically from all other members of the genus, and placed alone in the subgenus *Trachelocele* (Ellerman and Morrison-Scott 1951). Is this morphological divergence accompanied by significant molecular genetic divergence? 2. Groves (1983) proposed that the insular gazelles living on the Farasan Islands in the Red Sea should be treated as a separate species, namely *G. arabica*. However, Groves (1989) pointed out that *G. arabica* resembles *G. gazella* more closely than any other species. Based on skull measurements, Thouless and Al Basri (1991) proposed to consider gazelles from the Farasan islands as a subspecies of *G. gazella*, named *G. g. farasani.* Are electrophoretic data able to help differentiate between these two hypotheses? 3. At least five subspecies have been attributed to *Gazella gazella* sensu lato: *G. g. muscatensis, G. g. gazella, G. g. cora, G. g. farasani* and *G. g. erlangeri* (Groves 1989; Thouless and Al Basri 1991; Groves et al. 1994) based on morphological characteristics. Do some fixed allelic differences characterize any of these taxa, hence supporting the concept of separate gene pools in *G. gazella* sensu lato? 4. The taxonomic position of *G. rufifrons* is not clear. Groves (1975, 1985, 1988) described the Red-fronted Gazelle *G. rufifrons* with 7 subspecies: *rufifrons, laevipes, kanuri, tilonura, albonotata, nasalis* and *thomsoni.* The last three subspecies have usually been grouped in a different species: *G. thomsoni* (Dorst and Dandelot 1972; Corbet and Hill 1980; Nowak and Paradiso 1983). Is *G. thomsoni* a subspecies of *G. rufifrons*?

To address these questions, we have analysed by means of protein electrophoresis, samples of gazelle species from the Arabian peninsula, and 3 African species.

Material and methods

Origin of the animals

Gazella thomsoni albonotata (n = 8): eight animals from private collections in Saudi Arabia, all originating from Sudan. This taxon is called *G. rufifrons albonotata* by Groves (1985, 1988).

Gazella dorcas (n = 25): 16 individuals from different private collections in Saudi Arabia, 5 from Taif breeding center (National Wildlife Research Center, Saudi Arabia), and 4 from Thumama breeding center (King Khaled Wildlife Research Center, Saudi Arabia). The probable origin for all is Sudan. These animals would be representative of the taxon *G. dorcas isabella* mentioned by Groves (1969) and Alados (1986/1987).

Gazella subgutturosa (n = 30): 30 animals from Thumama center. They represent the subspecies *G. s. marica* (Nader 1989). This species is endangered (Iucn 1988) and limited to a very small geographic area in the Arabian peninsula, but is still common in Mongolia and in some parts of Russia (Groves 1988).

Gazella gazella gazella (n = 16): 16 individuals from the Thumama center. This gazelle is locally abundant in Northern Israel.

Gazella gazella cora (n = 7): 5 animals from Taif center and 2 from a private Saudi collection; they may have originated in Saudi Arabia. *G. g. cora* is rare and endangered in the mountains east of the Red Sea (Groves 1988).

Gazella gazella farasani (n = 5). 4 individuals from a private collection on Farasan Kebir island (Red Sea) and 1 wild gazelle from Farasan Kebir island. This taxon, distributed on Farasan islands, was previously called *G. arabica* by Groves (1985) but is more probably a subspecies of *G. gazella* (Thouless and Al Basri 1991). Its population status has been recently examined by Flamand et al. (1988), who found that these gazelles were still present in fairly large numbers.

Gazella gazella erlangeri (n = 15): 6 animals from Taif center, some of them thought to have been caught in the South of Saudi Arabia, 5 animals held in private collections in Saudi Arabia, 4 individuals from a pet shop in Djeddah. For the latter samples the origin was reported to be the region of Aden (Yemen). This subspecies has recently been described by Groves et al. (1994) after morphological and skull measurement comparisons with *G. g. cora* and *G. g. muscatensis*..

Gazella rufifrons (n = 1): 1 specimen from a private collection in Saudi Arabia. The origin of this sample is unknown. This gazelle could belong to the subspecies *kanuri* (synonym = *centralis*) or *laevipes* (synonym = *hasleri*) which are very similar.

Electrophoresis

Horizontal starch gel electrophoresis was performed on blood extracts collected by jugular puncture. An isotonic saline solution was added to the samples, and the plasma was separated from the red blood cells by centrifugation. Samples were duplicated for a reference collection and stored at –30 °C until electrophoresis was performed.

Electrophoresis, staining of the proteins, and scoring the results were conducted according to Pasteur et al. (1988). Many allozyme systems were assayed under different electrophoretic conditions, but only 16 loci that gave consistent results were retained (Tab. 1). Statistical and phylogenetic treatments were performed without taking hemoglobin into account, as the A and B subunits were not separated before running the gels. This prevented us from scoring the different alleles. Nevertheless, haemoglobin pattern appears very useful to distinguish *G. subgutturosa* as will be discussed further.

For each taxon, the percentage of polymorphic loci (P 95 %, i.e. a locus is considered polymorphic when the frequency of the most common allele is not higher than 0.95), mean number of alleles per locus (A), and mean heterozygosity (H) were calculated. Genetic distances between samples were estimated using formulae from Nei, "unbiased minimum distance" (1978) and Rogers (1972). The Arabian oryx (*Oryx leucoryx*) was used as an outgroup to root the tree for a phenetic analysis, with only 14 loci, because MPI and ACP could not be scored in this species. Allelic frequencies for Arabian oryx were published by Vassart et al. (1991). Phenetic analysis was performed via the Distance Wagner method (in BIOSYS-1, Swofford and Selander 1989), using the Rogers distance (1972) as modified by Wright (1978).

For cladistic analysis, allelic frequencies were coded as „locus-as-character“ (see Buth 1984). Alleles with low frequencies were kept even though this might have introduced a bias for small sample sizes. Data for oryx were not used here, as the information they bring after coding was too weak. Cladistic analysis was performed using PAUP 3.0 (Swofford 1990). Unordered option was used, and the consensus tree obtained with branch-and bound search after 1000 bootstrap replications was finally retained (threshold of 95 %).

Table 1. **Enzymes surveyed and electrophoretic buffers used**

Enzymes	Tissue	Locus	Buffer (pH)
GOT: Aspartate aminotransferase (EC 2.6.1.1)	RBC	1	TME 6.9/6.9
ACP: Acid phosphatase (EC 3.1.3.2)	RBC	1	TC 6.4/6.0
DIA: Diaphorase (EC 1.6.4.3)	RBC	1	TC 6.4/6.0
ES 10–14: Esterase 10 and 14 (EC 3.1.1.X)	RBC	2	TME 6.9/6.9
GLO: Glyoxalase (EC 4.4.1.5)	RBC	1	TBE 8.6/8.6
GPI: Glucose phophate isomerase (EC 5.3.1.9)	RBC	1	TC 6.4/6.0
LDH: Lactate dehydrogenase (EC 1.1.1.27)	RBC	1	TC 6.4/6.0
MDH: Malate dehydrogenase (EC 1.1.1.37)	RBC	1	TC 6.4/6.0
MOD: Malic enzyme (EC 1.1.1.40)	RBC	1	TC 6.4/6.0
MPI: Mannose phosphate isomerase (EC 5.3.1.8)	RBC	1	TC 6.4/6.0
NP: Nucleoside phosphorylase (EC 2.4.2.1)	RBC	1	TME 6.9/6.9
IPO: Superoxide dismutase (EC 1.15.1.1)	RBC	1	TC 6.4/6.0
ALB: Albumin	Serum	1	LiOH 8.3/8.1
ES 1: Esterase 1 (EC 3.1.1.X)	Serum	1	LiOH 8.3/8.1
TRF: Transferrin	Serum	1	LiOH 8.3/8.1

TME = Tris Maleate, TC = Tris Citrate, TBE = Tris Borate EDTA, LiOH = Lithium Hydroxyde.

Results

Among the 8 *Gazella* taxa, 8 loci were found to be polymorphic; mean heterozygosities (H) varied from 0 to 0.085, mean numbers of alleles per locus (A) from 1.0 to 1.31, and percentages of polymorphic loci (P) from 0 to 18.7 (Tab. 2). Of the eight polymorphic loci, only four exhibited significant variability: ES14, MOD, NP, and TRF (Tab. 2). NP with three alleles was polymorphic in five of seven taxa. Rogers (and Nei) genetic distances (Tab. 3) varied from 0.012 (0.001) to 0.304 (0.322) among taxa. IPO showed a fixed allelic difference between *G. thomsoni, G. dorcas* and *G. rufifrons*, on the one hand, and the five other taxa, on the other. GOT, DIA and GPI displayed minor variation, with a rare (less than 5 % frequency) allele in only one taxon each.

According to phenetic analysis using the Wagner method (Fig. 2), *G. subgutturosa* clusters together with the 4 samples of *G. gazella* sensu lato, and appears more similar to *G. g. erlangeri* mainly due to similar allelic frequencies at the NP locus. When hemoglobin data are considered, all *G. subgutturosa* samples had a unique pattern which distinguishes that species from all others (Fig. 4). On the phenogram, *G. rufifrons* lies in an intermediate position between *G. dorcas/G. thomsoni* and the cluster of *G. gazella/G. subgutturosa*.

For cladistic analysis, allelic frequencies were coded according to the qualitative method described in Buth (1984) (Tab. 4). The unrooted cladogram obtained after parsimony analysis (Fig. 3) confirms to a large extent the picture obtained with the phenetic analysis. Most of the samples in the *G. gazella/G. subgutturosa* group are characterized by minor autapomorphies (corresponding to low frequency alleles). *G. rufifrons* and the pair *G. dorcas/G. thomsoni* are clearly distinguishable from each other and from the *G. gazella/G. subgutturosa* group. Two synapomorphies separate *G. rufifrons* from each of the other two clusters.

Discussion

These results raise two points that require further discussion: the systematic implications of these allozyme data, and their implications for the conservation biology of the Arabian gazelles. It should be kept in mind that all the samples used here came from captive

Table 2. **Allelic frequencies for variable loci in 8 samples of *Gazella***

Locus	Allele	*G. thomsoni* (N = 8)	*G. dorcas* (N = 25)	*G. rufifrons* (N = 1)	*G. subgutturosa* (N = 30)	*G. g. gazella* (N = 16)	*G. g. cora* (N = 7)	*G. g. farasani* (N = 5)	*G. g. erlangeri* (N = 15)	*O. leucoryx*
GOT	80					0.03				
	100	1.00	1.00	1.00	1.00	0.97	1.00	1.00	1.00	
	120									1.00
DIA	80		0.02							
	100	1.00	0.98	1.00	1.00	1.00	1.0	1.00	1.00	
	120									1.00
ES 14	90									1.00
	100	0.37	0.36		1.00	1.00	1.00	1.00	1.00	
	105	0.63	0.64	1.00						
GPI	80									1.00
	100	1.00	1.00	1.00	0.95	1.00	1.00	1.00	1.00	
	120				0.05					
MOD	90									1.00
	100	0.37	0.32	1.00	1.00	1.00	1.00	1.00	1.00	
	110	0.63	0.68							
NP	60				0.90	0.25	0.07	0.40	1.00	
	100		0.90	1.00						1.00
	120	1.00	0.10		0.10	0.75	0.93	0.60		
IPO	30	1.00	1.00	1.00						
	100				1.00	1.00	1.00	1.00	1.00	
	120									1.00
TRF	90	0.12	0.96							1.00
	100	0.12	0.04	1.00	0.97	1.00	1.00	1.00	1.00	
	110	0.76			0.03					
H%		8.5	7.4	–	2.1	2.7	0.8	3.0	0.0	
A		1.25	1.31	–	1.19	1.12	1.06	1.06	1.00	
P95%		18.7	18.7	–	12.5	6.2	6.2	6.2	0.0	

N = sample size; H = mean heterozygosity; A = mean number of alleles per locus; P 95% = proportion of polymorphic loci.

populations, often derived from a few individuals, and therefore have probably been subject to sampling effect and subsequent inbreeding and genetic drift. Thus, they may not reflect allele frequencies of the parental populations and the results inferred from these samples should be taken with caution. Unfortunately, it is difficult to correct for these biases because the captive history of these samples is not well documented.

Our allozyme analysis does not support *G. subgutturosa* as an isolated taxon in the genus *Gazella*, or the concept of the subgenus *Trachelocele* for this species. This is in contradiction to the relationships suggested by Ellerman and Morrison-Scott (1951), Haltenorth (1963), and Groves (1969). Rather, *G. subgutturosa* appears to be related to *Gazella gazella* sensu lato. Among the protein systems considered here, hemoglobin appears to represent the only discriminative one between these two taxa (see Fig. 4).

The clustering of *G. thomsoni* and *G. dorcas* in the cladistic analysis (2 synapomorphies represented by ES14 and MOD) is surprising, since this was never suggested by studies of comparative morphology. From our data it is difficult to support the view of Groves (1975, 1985, 1988) or Lange (1972), who described *G. thomsoni* as a subspecies of *G. rufifrons*. However, chromosome numbers (58) also appear identical in *G. thomsoni* and *G. rufifrons* (Vassart, unpubl. results). Considering allelic frequency (see ES14) *G. rufifrons* could belong to the *G. thomsoni* group, but with a single specimen for *G. rufifrons*, this conclusion would be speculative.

There are no standard levels of genetic divergence associated with subspecies or species rank (see examples in Linnell and Cross 1991 and references in Cracraft 1989). However, our results suggest that several Arabian gazelles do belong to *Gazella gazella* sensu lato, namely, *G. g. erlangeri*, *G. g. farasani*, *G. g. gazella*, and *G. g. cora*. The small genetic distances between them are not larger than those found between geographic samples in other ungulates (see, for instance, Hartl and Reimoser 1988; Hartl et al. 1990). The position of *G. g. cora* well inside the *G. gazella* group does not agree with the hypothesis of *G. g. cora* being the Arabian representative of *G. dorcas* (Groves 1988). This has been confirmed by cytogenetic results: *G. g. cora*, *G. g. gazella*, *G. g. erlangeri* and *G. g. farasani* have 35 chromosomes in males and 34 in females (Vassart et al. 1993) whereas *G. dorcas* have 31 chromosomes in males and 30 in females.

Also, and contrary to the hypothesis of Groves (1985) and Groves and Lay (1985), *G. arabica* (our *G.*

Table 3. **Rogers (above diagonal) and Nei's (below diagonal) genetic distances between 8 taxa of *Gazella*, and *Oryx leucoryx***

	G. subgutturosa	*G. dorcas*	*G. g. gazella*	*G. g. farasani*	*G. g. erlangeri*	*G. thomsoni*	*G. g. cora*	*G. rufifrons*	*O. leucoryx*
G. subgutturosa	–	0.303	0.054	0.041	0.013	0.285	0.065	0.213	0.721
G. dorcas	0.254	–	0.295	0.292	0.304	0.128	0.298	0.209	0.577
G. g. gazella	0.030	0.245	–	0.012	0.055	0.239	0.014	0.162	0.719
G. g. farasani	0.016	0.240	0.000	–	0.043	0.248	0.024	0.171	0.718
G. g. erlangeri	0.001	0.264	0.040	0.024	–	0.291	0.066	0.214	0.727
G. thomsoni	0.226	0.099	0.176	0.182	0.243	–	0.225	0.131	0.697
G. g. cora	0.049	0.252	0.001	0.005	0.061	0.172	–	0.148	0.725
G. rufifrons	0.201	0.165	0.147	0.152	0.214	0.083	0.143	–	0.727
O. leucoryx	0.704	0.540	0.700	0.697	0.716	0.656	0.711	0.716	–

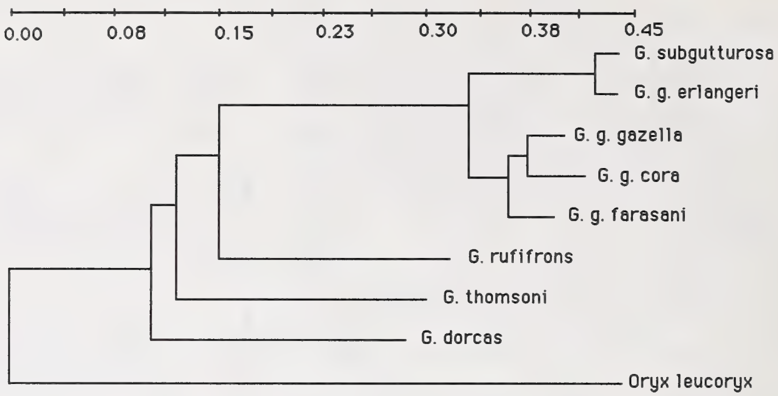

Fig. 2. Dendrogram derived from the Wagner procedure on the matrix of Rogers genetic distances

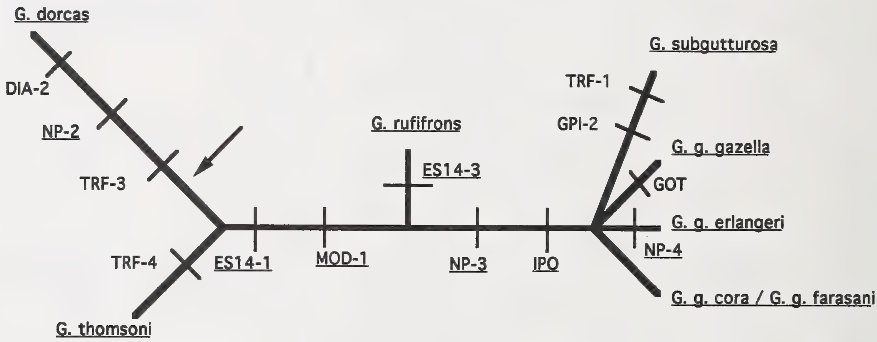

Fig. 3. Cladogram obtained with "locus as character" coding using branch-and-bound search after 1000 bootstrap replications. Synapomorphies are underlined, other characters are autapomorphies. The arrow points to the root leading to the outgroup (see Fig. 2)

Table 4. **Qualitative coding of allelic presence in sample data set from table 2**
See text for explanations

	GOT	DIA	ES14	GPI	MOD	NP	IPO	TRF
G. thomsoni	1	1	2	1	2	1	2	4
G. dorcas	1	2	2	1	2	2	2	3
G. rufifrons	1	1	3	1	1	1	2	2
G. subgutturosa	1	1	1	2	1	3	1	1
G. g. gazella	2	1	1	1	1	3	1	2
G. g. cora	1	1	1	1	1	3	1	2
G. g. farasani	1	1	1	1	1	3	1	2
G. g. erlangeri	1	1	1	1	1	4	1	2

g. farasani) should not be treated as a different species, but as a morphological and/or geographical race or subspecies of *G. gazella: G. g. farasani* as proposed by Thouless and Al Basri (1991).

As stated by Furley et al. (1988: page 48), "no common agreement has yet been reached on the number of genuine species within [*Gazella*]. . .", because of the considerable morphological variation shown by some species and the possibility of morphological

Fig. 4. Hemoglobin gel with TBE 8.6/8.6 buffer: R; *G. subgutturosa,* G; *G. gazella,* T; *G. thomsoni. G. dorcas* has the same patterns as *G. gazella*

convergence between taxa as illustrated by the cladistic analysis of skull and jaw characters of ALADOS (1986/1987). For this reason, we feel that a non-morphological approach, such as allozyme electrophoresis, should be used for reconstructing the systematics and evolutionary relationships of the gazelles. Examination of other species in the genus is needed, as well as the scoring of a greater number of loci.

With respect to conservation issues, GROVES (1989) stated that „for conservation purposes it is quite clear that each of the Arabian forms [*G. subgutturosa marica, G. gazella cora* and *G. dorcas saudiya*] represents a unique gene pool." Our data on the former two species support this view. But, as far as local forms are concerned, we have to deal with the "dilemma of subspecies" (RYDER 1986) when considering *G. g. gazella, G. g. cora, G. g. farasani,* and *G. g. erlangeri.* On the basis of our results, they are genetically very similar, however, from a conservation biologist's point of view, they might represent "unique gene pools," each one of which adapted to a particular local environment.

Among the different guidelines entering into consideration for selecting wild animals to be used for breeding purposes, genetic parameters such as mean heterozygosity and percentage of polymorphic loci should be taken into account. The data derived from our samples of *Gazella* (see Tab. 2) are similar to those found in natural populations of artiodactyls (see BACCUS et al. 1983; VASSART et al. 1991, for reviews). The mean heterozygosity for 184 species of mammals is 4.1 % ($\pm$ 3.5 SD) (NEVO et al. 1984), a value similar to the one observed for the three *Gazella* samples represented by more than 10 individuals in our study. On the other hand, the absence of genetic variability (despite the different origins of the samples) for *G. g. erlangeri* is potentially problematic. This gazelle is only known from captive individuals and there is no protected area on its supposed range (southwest of the Arabian peninsula). It is possible that the lack of polymorphism and heterozygosity resulted from the population bottleneck experienced by this subspecies. This could lead to inbreeding problems (O'BRIEN et al. 1983).

These results have to be confirmed by other molecular techniques such as mitochondrial DNA sequencing. This phylogenetic tool could be useful to differentiate all the different species of gazelles even if they are of recent origin, but could be of limited value at the subspecific level (CRONIN 1992).

Acknowledgements

This work was carried out under the patronage of HRH Prince SAUD AL FAISAL and Dr. ABUZINADA, Secretary of the National Commission for Wildlife Conservation and Development of the Kingdom of Saudi Arabia. The technical help of J.-F. AGNÈSE, G. BERREBI and L. DURAND during the establishment of the laboratory experiments has been invaluable. We wish to express our thanks to two anonymous reviewers and to M. A. CRONIN who provided valuable comments on the manuscript. We thank J. F. VOISIN for help in translating the summary into German. This is contribution 94-014 of the Institut des Sciences de l'Evolution (Montpellier, France).

Zusammenfassung

Genetische Verwandtschaft einiger Gazella-Arten: Eine Allozym-Untersuchung

Acht Arten der Gattung *Gazella* (Bovidae: Artiodactyla) wurden mit einer Allozymanalyse verglichen, um die genetische Verwandtschaft von Gazellen zu überprüfen, die derzeit in Saudi-Arabien zur Wiedereinbürgerung gezüchtet werden. Die elektrophoretische Untersuchung von 16 polymorphen Loci deutet darauf hin, daß mehrere ähnliche Taxa, nämlich *G. gazella gazella, G. gazella erlangeri, G. gazella farasani* und *G. gazella cora* zur gleichen Art *G. gazella* sensu lato gehören. Vier andere Arten sind davon deutlich genetisch verschieden: *G. thomsoni* und *G. dorcas*, die genetisch ähnlich sind, sowie *G. rufifrons* und *G. subgutturosa*. Die Untergattung *Trachelocele*, der die letzte Art aufgrund morphologischer Merkmale zugeordnet worden ist, konnte aufgrund der Allozymvergleiche nicht bestätigt werden. Die Polymorphismus- und Heterozygotie-Grade der Gattung *Gazella* waren insgesamt den bei anderen Säugern gefundenen Werten ähnlich. Die Ergebnisse werden im Hinblick darauf diskutiert, welche Schlußfolgerungen sich aus den genetischen Untersuchungen für ein angestrebtes Schutzprogramm ergeben.

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Authors' addresses: Marc Vassart, Ecole Nationale Vétérinaire de Toulouse, 23 chemin des Capelles, F-31076 Toulouse, France; Laurent Granjon, Museum National d'Histoire Naturelle, 55 rue Buffon, F-75005 Paris, France; Arnaud Greth, National Wildlife Research Center, P. O. Box 1086, Taif, Saudi Arabia; François M. Catzeflis, Université de Montpellier II, Institut des Sciences de l'Evolution, URA 327 CNRS, F-34095 Montpellier, France

Z. Säugetierkunde 59 (1994) 246–251

ISSN 0044-3468

Springbok, *Antidorcas marsupialis* (Zimmerman, 1780) from the past

By Ina Plug

Department of Archaeozoology, Transvaal Museum, Pretoria, South Africa

Receipt of Ms. 29. 11. 1993
Acceptance of Ms. 17. 6. 1994

Abstract

Analysed 6000 springbok, *Antidorcas marsupialis* (Zimmerman, 1780), bone fragments from an archaeological site in South Africa. This enabled deductions on herd composition and seasonality of springbok from the period before settled farming and large scale hunting disrupted herd mobility and reduced numbers. Techniques of osteomorphology and osteometry were used to compare the archaeological bone with modern skeletal material. The results show that the excavated remains are predominantly from foetal, neonate and adult individuals. On average the animals from the archaeological samples were somewhat smaller than modern springbok females, suggesting that most of the animals in the archaeological samples were also females. The age profiles and the large numbers of foetal and neonate individuals indicate that the assemblage was taken from lambing herds. Climatological and environmental conditions of the region indicate that these herds visited the area during spring and early summer on a seasonal basis. They were not part of the occasional mass movements, or smaller mixed herds, as such herds consist of animals of both sexes and all ages.

Introduction

Archaeozoological and palaeontological studies provide information on the anatomy of wild animals from the past, but most samples are too small to allow deductions on herd composition, behaviour and average sizes of the animals. The large sample of springbok, *Antidorcas marsupialis* (Zimmerman, 1780), bones from an archaeological site provided an unique opportunity to determine if such deductions can be made on larger samples, and to compare the results with those of modern springbok studies and historical observations.

The distribution of springbok in South Africa is mainly restricted to game reserves and farms where herd mobility and herd size are limited. Little is known about structure and behaviour of free roaming herds in the past. Until 1950, in the Kalahari Gemsbok Park and Botswana, springbok sporadically congregated in their thousands and mega-migrations occurred (Conwright-Schreiner 1925; Child and Le Riche 1969; Bigalke 1972). Springbok herds of the Kalahari Gemsbok Park, consist of individuals of both sexes and all age groups, with the exception of neonates. These herds are small in winter and larger in summer when the grazing is good. At the start of the lambing season females congregate and male animals of six months and older are driven off to form bachelor herds (Skinner and Smithers 1990). A few territorial males remain with the females. The lambing season may vary from region to region, but most lambs are born between September, at the beginning of the rainy season, and January, with the highest peak in October. Females of a particular herd usually drop their lambs within one or two months (van Zyl and Skinner 1970; Skinner et al. 1974; Skinner et al. 1977).

Material and methods

The springbok bones, other faunal remains and artefacts of hunter-gatherer communities were retrieved from Abbot's Cave (ABB) in the Seacow Valley, Karoo, South Africa, (31°27′ S, 24°39′ E)

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(Fig.). Most of the deposit dates to between 1270 and 1682 AD, predating European contact and the establishment of demarcated farms (Sampson and Vogel 1989; Sampson et al. 1989; Plug 1993). The samples therefore reflect the past fauna endemic to the region.

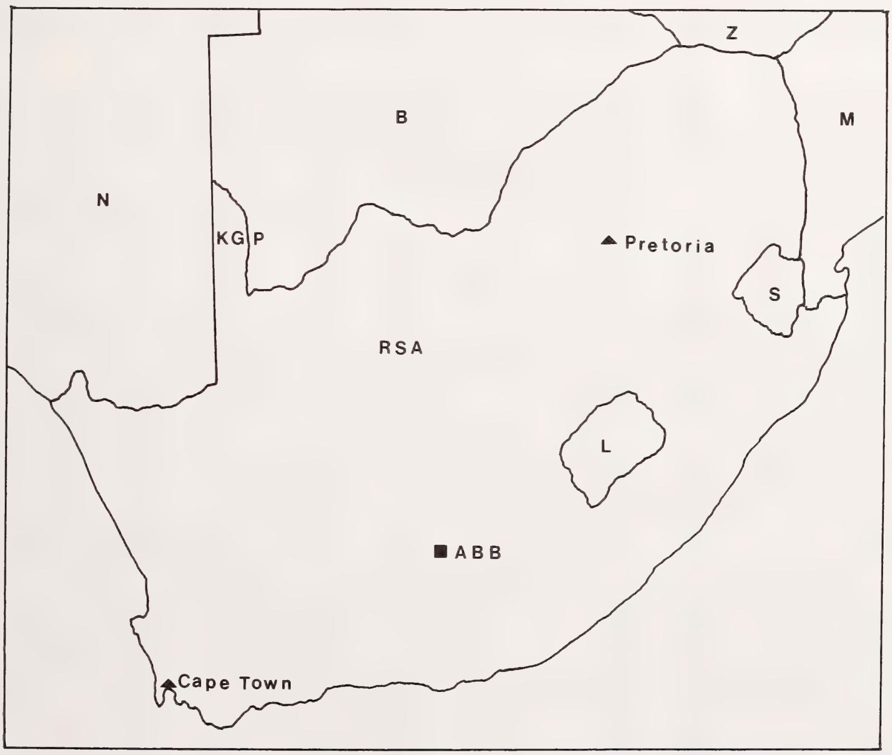
Early historical records of the 18th century only make passing reference to the wild animals in the valley. However, in his diary, Jacob Gordon (Raper and Boucher 1988) mentions that small herds of springbok remained in the valley for most of the year, but that larger herds (not mega-herds) moved in from September to November, migrating southwards. He observed that most lambs were dropped in August and September (Raper and Boucher 1988). Mating must therefore have taken place at the end of the rainy season in late summer and autumn, when ewes would have been in optimum condition.

The heavily fragmented ABB macrofaunal sample consists of over 142 000 fragments of which 6.6 % could be identified, representing 46 different species. Of the 9415 identified fragments 4586 (49 %) are from springbok and 1418 (15 %) from probably springbok. Determinations were made by using the comparative skeletal collections of the Transvaal Museum and the osteomorphological criteria for fragments of springbok (Plug and Peters 1991) and for modern springbok skeletons (Peters and Brink 1992).

Measurements were taken with dial calipers to the nearest 0.1 mm. Only bones from fully adult animals were measured according to procedures defined by von den Driesch (1976) and Peters (1988). Means and standard deviations were calculated. Only 337 post-cranial springbok fragments were measurable, including complete as well as partially complete bones, mostly carpals, tarsals and phalanges.

The measurements of modern springbok adults of known sex (Peters and Brink 1992) were compared to those of the archaeological sample. The table lists the measurements of the archaeological post-cranial elements that number five or more, as well as the relevant measurements of modern springbok.

No detail information exists on the ages of springbok in relation to skeletal development. Based on



Map of southern Africa showing the position of Abbot's Cave (ABB). N = Namibia; B = Botswana; Z = Zimbabwe; M = Mozambique; RSA = Republic of South Africa; L = Lesotho; S = Swaziland; KPG = Kalahari Gemsbok Park

Table. **The measurements of postcranial skeletal elements of archaeological and modern springbok where sample size is five or more**

The measurements of the modern springbok are taken from Peters and Brink (1992)

	Archaeological sample			Modern females			Modern males		
	n	x	s	n	x	s	n	x	s
				Os carpi radiale					
GD	26	20.0	1.24	26	19.7	1.21	20	21.1	1.46
GH	26	12.6	1.55	26	13.4	1.00	20	14.3	1.17
BFd	26	10.8	1.52	26	9.9	0.64	20	10.7	0.93
				Os carpi intermedium					
GD	9	19.6	0.60	25	19.0	1.32	18	20.4	1.36
GH	9	12.8	0.83	25	12.7	1.09	18	13.7	1.11
				Os carpi ulnare					
GL	16	18.4	1.15	26	18.4	1.06	18	20.1	1.33
				Os carpale II + III					
GB	31	14.0	1.93	25	14.6	0.96	19	15.7	1.13
GD	31	15.1	2.36	25	15.9	0.96	19	16.9	1.32
				Os carpale IV					
BFd	42	10.4	0.62	25	10.4	0.73	18	10.8	2.66
GH	42	11.1	0.86	25	10.9	0.89	18	11.1	2.67
				Os metacarpale III + IV					
Bd	5	23.5	1.35	26	22.4	1.43	19	20.5	1.60
Dd	5	18.5	0.62	26	18.0	1.32	19	24.3	1.08
				Patella					
GL	5	26.4	2.40	26	28.5	2.15	20	30.0	2.21
GB	5	22.3	4.29	26	25.1	2.05	20	26.1	3.35
				Os malleolare					
GD	30	15.0	1.01	23	15.4	1.16	19	16.0	1.25
				Talus					
GLl	30	29.9	1.73	29	30.5	1.98	20	31.7	2.53
GLm	30	27.6	1.36	29	28.7	1.82	20	29.5	2.08
Dl	30	17.2	0.86	29	17.6	1.10	20	18.3	1.48
Bd	30	18.5	1.17	29	18.9	1.22	20	19.6	1.43
				Os centroquartale					
GB	5	24.3	0.79	27	24.3	1.57	20	25.5	1.71
GD	5	23.1	1.11	27	26.1	1.61	20	27.6	1.99
				Os tarsale II + III					
GD	28	17.9	1.28	24	17.7	1.52	20	18.5	1.97
				Os metatarsale III + IV					
Bd	7	24.6	0.63	26	23.4	1.43	19	25.2	1.57
Dd	7	18.6	0.56	26	18.5	1.63	19	19.7	0.98
				Phalanx proximalis pedis					
GLpe	6	40.6	3.07	25	43.4	2.89	19	46.1	4.10
BP	6	11.6	0.57	25	11.9	0.78	19	12.3	0.89
Bd	6	10.6	0.28	25	10.1	0.79	19	10.6	0.80
SD	6	9.0	0.33	25	8.8	0.78	19	9.3	0.75
				Phalanx media manus					
GL	7	25.4	0.74	23	25.5	1.72	19	27.2	2.51
BP	7	10.3	0.56	23	10.1	0.64	19	10.9	0.89
Bd	7	8.7	0.64	23	8.6	0.63	19	9.2	0.67
SD	7	7.6	0.62	23	7.1	0.51	19	7.7	0.61

Table (continued)

	Archaeological sample			Modern females			Modern males		
	n	x	s	n	x	s	n	x	s
				Phalanx media pedis					
GL	7	23.6	0.39	24	25.0	1.68	19	26.3	2.23
BP	7	10.3	0.29	24	10.1	0.70	19	11.0	2.03
Bd	7	8.9	0.47	24	8.6	0.73	19	9.0	0.61
SD	7	7.5	0.38	24	7.2	0.55	19	7.6	0.71
				Phalanx distalis					
DLS	72	27.7	1.94	20	30.2	3.21	18	33.0	3.99
Ld	72	23.4	1.81	20	25.4	2.94	18	28.2	3.76
Hp	67	17.0	1.69	20	17.5	1.40	18	19.0	1.35
BFp	72	8.6	0.70	20	8.4	0.68	18	8.8	0.62

n = number; x = mean; s = standard.

tooth eruption, tooth wear and epiphyseal fusion the following relative age categories, with brief descriptions, are distinguished (Plug 1988, 1993):
Foetal/neonate: deciduous teeth unerupted, unfused proximal radius, os centroquartale and metapodials (longitudinally, proximally and distally), bones spongy;
Neonate/juvenile: deciduous teeth erupting/just in wear, M 1 unerupted/erupting, proximal radius, os centroquartale and metapodials longitudinally still unfused or beginning to fuse;
Juvenile: deciduous teeth and M 1 in wear, M 2 erupting, metapodials longitudinally fused, most epiphyses unfused, articulation surfaces well defined;
Sub-adult: M 2 in wear, M 3 erupting, heavy wear on deciduous teeth, most epiphyses beginning to fuse;
Young adult: M 3 in wear, most deciduous teeth replaced, most epiphyses fused;
Adult: all permanent teeth present and in wear, heavy wear on M 1, all epiphyses strongly fused;
Mature: heavy wear on all teeth, no central islands on M 1 and disappearing on M 2 and M 3;
Aged: no central islands on M 3, M 1 and M 2 worn down to roots, ossification of muscle attachments and cartilage.

Pelvis fragments were used to determine the sex of adult individuals. No other bones were well enough preserved to allow sexing.

Results

The springbok bone sample contains an unprecedented amount, almost 15 %, of foetal/neonate bones and an additional 2 % neonate/juvenile bones. This is the first time that so many bones from such young (nondomestic) animals have been found in a South African archaeological site. Foetal animals are seldom represented and neonates only occasionally, but juveniles are usually well-represented in most assemblages. As foetal and neonate bones are extremely fragile, they may even be underrepresented in the ABB sample. The other age categories represented are: 1 % sub-adult, less than 1 % young adult, 75 % adult, 4 % mature, and 2 % aged. There were no juveniles present in the sample.

The measurements of the archaeological sample fall mainly within the range of those of modern females (Tab.). Some of the archaeological bone, phalanges in particular, are somewhat smaller on average, than modern females, but the differences are small and not consistent. Of the 40 pairs of mean values, the mean of the archaeological measurements is smaller than the modern mean of females in 19 cases, larger in 18 cases and equal in three. Compared to modern males, the archaeological sample is smaller in 36 cases, larger in one and equal in three.

The standard deviations of the measurements of the archaeological sample were also compared with those of the modern sample. This shows that in 26 and 30 of the measurements the archaeological sample has a smaller standard deviation and in 14 and 10 a larger standard deviation than the modern female and male samples respectively. This

indicates that the animals from the ABB herds were slightly more homogenous in size than those of the modern sample. This result is not unexpected as the modern sample consists of animals that were obtained from different geographical regions.

Osteomorphologically it was not possible to distinguish with confidence between the sexes, as attempts to determine sex were hampered by the fragmented nature of the assemblage. Subsequently only eight females and two males were identified on pelvis fragments, but as male pelves are more robust than those of females and are less susceptible to natural attrition, females are probably underrepresented. The possibility that there is overlap between young males and large females should be considered. The young adult category is poorly represented ruling out the possibility that young males (or young females) influenced the sample significantly. It can therefore be argued that, combined with the high incidence of foetal/neonates, the majority of the adult springbok were females.

Discussion

Archaeological faunal samples have inherent limitations for research, related to fragmentation, preservation and attrition. Nevertheless, the results show that even samples as heavily fragmented as the ABB assemblage, have research value.

The age structure of the springbok from ABB suggests that the majority of the animals did not come from mixed herds or migrating mega-herds. Foetal/neonate animals are not part of the former and can be expected in small numbers only, in the latter, whereas the juvenile, sub-adult and young adult categories should be better represented in both herd types.

The results indicate that females were more frequently hunted than males, while the large foetal/neonate component shows that they were culled from female lambing herds. The hunters of ABB appear to have been familiar with the migratory and breeding cycle of the springbok and deliberately preyed on pregnant and lactating females as these would have had a relatively high body fat content.

The ABB deposits give no indication of major climate changes within the past 1000 years (Bousman 1991). It would therefore be reasonable to assume that the prime mating season for springbok was in late summer and autumn when grazing in this region is at its best after the summer rains. As a result the majority of foetal and neonate springbok from ABB would have been born in August–September, as has been observed in the 18th century.

The age categories of the springbok from ABB indicate that the herds did not remain in the vicinity long after lambing. Juvenile, sub-adult and young adult animals are either absent or poorly represented, suggesting that the new crop of lambs matured elsewhere. The area near ABB would have been attractive to springbok in August–September, as it has a small seasonal wetland that could have supported some good grazing towards the end of winter.

In summary, the springbok living in the Seacow Valley before settled farming, usually dropped their lambs in early spring (August to September). They congregated in female herds for the occasion, but did not remain in the area. The herds seem to have had some mobility, probably on regional scale, to optimize grazing opportunities.

Acknowledgements

I am grateful to Prof. C. G. Sampson of Southern Methodist University in Dallas and the South African Museum in Cape Town. My thanks also go to the Foundation for Research Development for their financial support.

Zusammenfassung

Springböcke, Antidorcas marsupialis (Zimmerman, 1780), aus vergangenen Zeiten

Die Entdeckung einiger tausend Springbockknochen (*Antidorcas marsupialis* Zimmerman, 1780) von einer archäologischen Fundstelle in der Karoo, Südafrika (13.–17. Jahrhundert), bot die Gelegenheit, Populationsstruktur, Körpergröße und saisonale Fluktuationen der Art zu untersuchen, bevor Farmgründungen und starke Bejagung das Wanderverhalten störten und die Bestände reduzierten. Die ausgegrabenen Knochen stammen überwiegend von ungeborenen und ganz jungen Individuen und von ausgewachsenen Weibchen. Osteometrische Vergleiche mit rezenten Springbockweibchen zeigten, daß die damaligen Tiere im Durchschnitt etwas kleiner waren. Das Vorkommen zahlreicher Feten und Jungtiere macht es wahrscheinlich, daß die Herden das Gebiet und die Fundstelle im Frühjahr und zum Sommeranfang aufsuchten und hier dann gejagt wurden.

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Author's address: Ina Plug, Department of Archaeozoology, Transvaal Museum, P. O. Box 413, Pretoria 0001, South Africa

Z. Säugetierkunde 59 (1994) 252–254

ISSN 0044-3468

WISSENSCHAFTLICHE KURZMITTEILUNG

Marmosops scapulatus Burmeister, 1856, and the brown mutation in didelphids (Marsupialia)

By Meika A. Mustrangi

Museum of Vertebrate Zoology, University of California at Berkeley, Berkeley, USA

Receipt of Ms. 23. 4. 1993
Acceptance of Ms. 15. 11. 1993

A female mouse opossum of the genus *Marmosops* Matschie, 1916, showing an unusually pale coat color was collected in the Atlantic Coastal Forest in Brazil in July of 1992 (see figure). The site is the Intervales biological reserve in the State of São Paulo, 24° 20′ S, 48° 25′ W. The animal was captured in a Sherman trap tied to a tree limb at approximately 1.5 m from the ground in primary forest habitat. It was immediately recognized for its unusual coloration since the only species of *Marmosops* known to occur in all southeastern Brazil, *M. incanus*, shows an invariably dark gray-brown coloration above and creamy white below (Emmons 1990). The pale female is light cinnamon-brown dorsally, corresponding to a score of 7.5 YR 4/4 in the Munsell system of color (Munsell Color Company 1976). The underparts are of a pinkish, creamy white. The dorsal coloration of *M. incanus* (as measured from the other individuals collected in Intervales) corresponds to a score of 10 YR 2/1. The pale individual was prepared as skin, skull, and partial skeleton and will be deposited at the Museu de Zoologia da Universidade de São Paulo. A sample of liver tissue was preserved in ethanol for molecular analyses. Female mouse opossums are generally much smaller than males, but old females may reach the size of males (Tate 1933). The pale female was a very old individual (age class 7 of Tribe 1990), and equalled in size the adult males of *M. incanus* collected at that locality.

Not surprisingly, new species of mammals are still being described in South America (e.g. the marmoset, *Callithrix maues*, of the Amazon basin by Mittermeier et al. 1992; the lion tamarin, *Leontopithecus caissara*, of the Atlantic Forest by Lorini and Persson 1990; three new species of gracile mouse opossums, genus *Gracilianus*, from the forested Andean slopes by Hershkovitz 1992). To evaluate the possibility that the pale female represented a new species of *Marmosops*, I sequenced the first 380 base pairs of the mitochondrial cytochrome b gene for 4 of the individuals collected at that locality. I also looked for differences in cranial characters. No significant differences were found among the several skulls, apart from size-related ones. The comparison of the cyt. b sequences revealed the presence of two haplotypes, differing by only one silent, third position transition. The pale female and an individual of normal coloration had one haplotype, with the other 2 individuals showing the other. Sequence variation (calculated as the number of varying sites divided by the total number of sites compared), therefore, amounts to 0.3 percent, well within the range of intrapopulation variation for this gene observed in other species (Smith and Patton 1991).

DNA sequencing was a quick way to test the hypothesis that the pale female represented a different, so far undescribed, species of *Marmosops*. Since it is not a new species, its unusual coat color might be an age-related phenomenon, or might represent a rare mutation. The first alternative seems unlikely since no other individual with the same

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contrasting coloration has ever been collected in that area, despite recent extensive collecting efforts (De Vivo, pers. comm.).

Hartman (1921, 1922) reported on a brown or cinnamon variety of the Virginia opossum (*Didelphis virginiana*). In those individuals, the underfur was of a "uniform and delicate light brown" instead of black. Hartman (1921, 1922) associated this color morph with the so-called brown mutation in house mice. Currently, this recessive allele is known to occur in several orders of mammals (Searle 1968). The predominant effect of the b allele is to change the nature of eumelanin from a black to a brown pigment, and thus the coat color from gray to cinnamon brown (Silvers 1979). As expected in a brown individual, the pigment granules in the pale *M. incanus* female are of a brownish color, instead of the black color displayed by the typically colored *M. incanus* individuals.

Marmosops incanus Lund, 1840, collected in Intervales, Brazil: an adult male (left) and the brown female (right)

In a recent study, De Oliveira et al. (1992) reported on the results of their analysis of pelage variation in this same species. The authors concluded that the different pelage types of *M. incanus* represent different ontogenetic and sexually dimorphic states, and not seasonal (summer and winter) pelage types as it was previously believed (e.g. Emmons 1990). The authors agree with Emmons (1990) in synonymizing *M. scapulatus* Burmeister, 1856, to *M. incanus*, believing that it had been described as a different species on the basis of the misinterpreted pelage variation.

Besides the pelage type, however, the *M. scapulatus* male individual is also distinct from other *M. incanus* individuals by its general coloration, originally described by Burmeister as being composed of hairs "at base slate gray, then pale yellow-red, and last cinnamon" (Tate 1933). It seems reasonable to argue that the *M. scapulatus* individual and the pale female described here represent two independent manifestations of the same rare, recessive allele, separated in time by at least 136 years.

Interestingly enough, a female *Philander* of a similar, pale coloration was recently collected in the Atlantic Forest by P. Hershkovitz. The female *Philander* later gave birth to several young of normal, dark coloration. Pending on a closer study of this specimen, it raises to three the didelphid genera known to present the brown mutation, making it more common and widespread in didelphid marsupials than presently known.

Acknowledgements

I would like to thank James L. Patton, William Z. Lidicker, Sergio F. dos Reis, Kevin Burns, and Albert D. Ditchfield for critically reviewing and helping improve this manuscript. This study was funded by a graduate studies' fellowship from FAPESP (Brazil).

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Author's address: MEIKA A. MUSTRANGI, Museum of Vertebrate Zoology, 1120 Life Sciences Building, University of California at Berkeley, Berkeley, CA 94720-0001, USA

BUCHBESPRECHUNGEN

NIETHAMMER, J.; KRAPP, F. (Hrsg.): **Handbuch der Säugetiere Europas**. Bd. 3/1: Insektenfresser, Primaten. Wiesbaden: Aula-Verlag 1990. 524 S., 141 Abb., 133 Tab., 328,– DM. ISBN 3-89104-027-X

Band 3/1 des Handbuches der Säugetiere Europas behandelt die Insectivoren-Familien der Igel, der Maulwürfe und der Spitzmäuse sowie den Berberaffen, den einzigen hier in Frage kommenden Primaten. Der Umfang von 524 Seiten machte es erforderlich, den ursprünglich für diesen Band mit eingeplanten Hasenartigen einen weiteren Band zu widmen. Neben den Herausgebern, von denen besonders J. NIETHAMMER für zahlreiche Kapitel als Autor tätig war, haben mitgewirkt: M. GENOUD, J. HAUSSER, H. HOLZ, R. HUTTERER, E.-A. JUCKWER, T. MADDALENA, H. PIEPER, F. SPITZENBERGER, D. STARCK, S. SULKAVA, P. VLASAK und P. VOGEL.

Auch bei diesem Band wurde die bewährte Gliederung beibehalten. Nach einer kurz gehaltenen Einführung folgt der Hauptteil mit je einer knappen Vorstellung der Ordnungen Insectivora und Primates, an die sich die zu ihnen gehörigen Taxa anschließen. Hierbei wird für Familien und Gattungen ein einheitliches Gliederungsschema verwendet (Diagnose; Angaben zur Verbreitung, zu Umfang und Gliederung der Familien bzw. der Gattungen, zur Paläontologie; besondere Merkmale); Gattungs- und Artenschlüssel beschließen die Familien- und Gattungsabschnitte und leiten zu den Kapiteln der einzelnen Arten (26 Insectivoren- und eine Primatenart) über. Hier findet sich jeweils wieder eine Diagnose (u. a. Karyotyp), auf die Ausführungen zur Taxonomie, zur Morphologie („Beschreibung", die sich nicht auf Skelettmerkmale beschränkt), zur Verbreitung, zur Merkmalsvariation, zur Paläontologie, zur Ökologie, zur Jugendentwicklung und zum Verhalten folgen. Für nahezu jede der Arten und ebenso für die höheren Taxa gibt es eine eigene, zum Teil sehr umfangreiche Bibliographie (für *Sorex araneus* mehr als zehn Seiten); am Ende des Bandes folgt darüber hinaus noch ein „Allgemeines Literaturverzeichnis". Eine Fülle von Abbildungen (Zeichnungen von Schädeln, Zähnen, postcranialer Skeletteile sowie anderer Merkmale der Formen; Diagramme; Verbreitungskarten) und eine große Anzahl von Tabellen ergänzen die Texte. Unter letzteren sollen diejenigen mit individuellen Maßen der Arten von unterschiedlichen Fundorten besonders erwähnt werden; diese zum Konzept des Handbuches gehörenden Tabellen beanspruchen zwar viel Raum, zeigen aber auch die besondere Mühewaltung der Autoren und wären nicht durch Hinweise auf Originalliteratur zu ersetzen.

Wissenschaftliche Kompetenz und Ausstattung dieses Bandes sind so hervorragend wie diejenigen der vorherigen. Die strikte Einhaltung des Gliederungsschemas erleichtert Orientierung und Arbeit in diesem Werk, dessen große Informationsfülle in knapp gefaßten, gut lesbaren Texten dargeboten wird. Den Autoren, dem Verlag und im besonderen den Herausgebern ist für diese besonders wichtige Fortsetzung der Handbuchreihe zu danken, die auf lange Zeit einen festen Platz in den Bibliotheken nicht nur der europäischen Mammalogen einnehmen wird. H. SCHLIEMANN, Hamburg

ECKERT, M.; HERTEL, W. (Hrsg.): **Praktikum der Tierphysiologie**. Jena, Stuttgart: Gustav Fischer Verlag 1993. 312 S., 138 Abb., 44 Tab., 58,– DM. ISBN 3-334-60438-1

Der vorliegende Band enthält zahlreiche Anleitungen zu experimentellen Arbeiten auf den wichtigsten Gebieten der Tierphysiologie und Verhaltensbiologie. Die Versuche, die offensichtlich von den Autoren gründlich in der Lehre erprobt worden waren, sind so konzipiert, daß sie bei entsprechender Betreuung auch von unerfahrenen Experimentatoren durchgeführt werden können.

Die Beschreibung der einzelnen Aufgaben ist gut gelungen. Nach einer kurzen Einführung in die Theorie folgt eine anschauliche Erklärung der Versuchsdurchführung. Zahlreiche Abbildungen der für den Versuch benötigten Präparate, Skizzen der Versuchsanordnungen sowie grafische Darstellungen repräsentativer Versuchsergebnisse geben eine wertvolle Hilfe bei der Durchführung und Auswertung der Versuche. Zur statistischen Aufarbeitung der Versuchsergebnisse erhalten die Praktikumsteilnehmer nützliche Hinweise im Abschnitt 1.5, in dem die wichtigsten Methoden der Statistik erläutert werden.

Die Praktikumsanleitung enthält weiterhin Hinweise zur Zucht und Haltung verschiedener Versuchstiere, zum Umgang mit gefährlichen Stoffen (Arbeitsschutz) sowie zu den physikalischen Grundlagen der elektrophysiologischen Meß- und Registriertechnik. In diesem allgemeinen Teil wird auch auf die gesetzlichen Bestimmungen zur Durchführung genehmigungspflichtiger bzw. anzeigepflichtiger Tierversuche hingewiesen (Tierschutzgesetz, Naturschutzgesetz). Zu diesem Abschnitt wäre allerdings zu bemerken, daß erstens bei der Genehmigung von Tierversuchen zu Ausbildungszwecken zur Zeit sehr restriktiv verfahren wird, und daß zweitens auch genehmigte bzw. angezeigte Versuche an Wirbeltieren von den Studierenden häufig abgelehnt werden. Erfahrungsgemäß werden dagegen Versuche an Evertebraten von den Studierenden im allgemeinen akzeptiert. Diese Schwierigkeiten werden jedoch in der vorliegenden Praktikumsanleitung berücksichtigt; es werden in nahezu

allen Abschnitten genügend Versuche an Wirbellosen angeboten, so daß auf Experimente an Vertebraten weitgehend verzichtet werden kann.

Das „Praktikum der Tierphysiologie“ stellt eine gut abgestimmte Ergänzung des von PENZLIN verfaßten Lehrbuches der Tierphysiologie dar. Die vorliegende Praktikumsanleitung kann deshalb Lehrenden und Lernenden gleichermaßen empfohlen werden. W. WÜNNENBERG, Kiel

TAMARIN, R. H.; OSTFELD, R. S.; PUGH, S. R.; BUJALSKA, G. (eds.): **Social Systems and Population Cycles in Voles**. ALS Advances in Life Sciences. Basel, Switzerland: Birkhäuser Verlag 1990. 229 pp. 62,– sFr. ISBN 3-7643-2437-6 or 0-8176-2437-6

The themes presented by the two editors at the two International Theriological Congresses in Edmonton (Social system in *Microtus*) and in Rome (the relationships between social systems and population dynamics in Microtine rodents) led to the edition of the present volume. In addition to 4 overview articles, there are 10 papers dealing with *Microtus*-species, 5 with *Clethrionomys*-species and one paper on *Arvicola terrestris*. The critical remarks and the emphasis put on the flexibility of the social organization of Arvicolidae in the overview articles deserve special attention. Of the *Microtus*-species, *M. agrestis* is the only European species mentioned. Best represented of the genus *Clethrionomys* is *C. glareolus*. Both species were investigated in northern European habitats.

In the species studied, the relationships between the mating system, crowding, natural history, territoriality, predation by specialists and the impact of the changing in density and population dynamics are discussed.

It was not possible to agree upon a common concept regarding the relationship between certain social systems and population dynamics. However, numerous ideas about different methods and results, which could enhance a fruitful discussion, are presented. This is the reason why this collection of papers is a rich source of information especially for population biologic-ethological seminars, as this reviewer has already experienced in a eco-theriological seminar. R. SCHRÖPFER, Osnabrück

SCHALLER, O. (ed.): **Illustrated Veterinary Anatomical Nomenclature**. In cooperation with G. M. CONSTANTINESCU, R. E. HABEL, W. O. SACK, P. SIMOENS, N. R. DE VOS. Stuttgart: Ferdinand Enke Verlag 1992. VIII, 614 pp., 280 plates including 1316 illustr., 148,– DM. ISBN 3-432-99591-1

This book is a most effective medium for all scientists to obtain correct anatomical nomenclature as approved by the “International Anatomical Nomenclature Committee”. The lists published as “Nomina Anatomica Veterinaria” confront the reader only with terms, but do not give illustrations of the listed structures. This volume, however, which was edited by an Austrian veterinary anatomist with the cooperation of two Belgian and three US-American specialists, helps the reader by illustrating the relevant anatomical structures and including them in their topographical surrounding. Reference is made to seven domestic mammalian species, namely, cat, dog, pig, ox, sheep, goat, and horse, but not to birds.

On the right hand pages very clear and informative line drawings are given and the structures within them are labelled with numbers. On the opposite left hand pages the scientific names and very often their Anglisized versions, are listed according to the above-mentioned numbers, followed by very short explanations in English. The book is subdivided according to eleven subheadings: Regions of the body, osteology, arthrology, myology, splanchnology, angiology, nervous system, sense organs, common integument, parts of the body, and general terms.

Reference to this volume can be made in three different ways: A scientific name can be brought into its topographical context with the help of an alphabetical index (39 pages) at the end of the book. Alternatively, a user who has seen the structure during dissections, can refer to the illustrations of the respective body system, which is indicated at the page heading and will then be able to identify the name of the structure. The third alternative includes consulting the tables of names and obtaining information concerning the topographical situation of the structure.

The spelling in ambiguous cases is given in both the American and British forms (e.g., esophagus [oesophagus]). Terms of orientation are used that make sense in quadrupedal mammals, but are generally not used by specialists on human gross anatomy (V. cava cranialis instead of V. cava superior).

This book is a very systematic illustrative dictionary of anatomical terms that is easy to handle and very well produced. Hopefully, not only veterinarians, but also mammalogists in general will make use of this publication, which presents a sound and widely applicable nomenclature of the gross anatomy of terrestrial mammals. P. LANGER, Gießen

Erscheinungsweise und Bezugspreis 1994: 6 Hefte bilden einen Band. Jahresabonnement Inland: DM 378,– zuzüglich DM 13,80 Versandkosten; Jahresabonnement Österreich: öS 2949,– zuzüglich öS 164,– Versandkosten; Jahresabonnement Schweiz: sfr 364,– zuzüglich sfr 21,– Versandkosten; Jahresabonnement EG-Binnenmarkt-Länder mit USt-ID-Nr.: DM 353,27 zuzüglich DM 19,63 Versandkosten; Jahresabonnement EG-Binnenmarkt-Länder ohne USt-ID-Nr. und Drittländer: DM 378,– zuzüglich DM 21,– Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey GmbH & Co. KG, Spitalerstraße 12, D-20095 Hamburg, Bundesrepublik Deutschland, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde“ erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Z. Säugetierkunde 59 (1994) 4, 193–256

Vol. 59 (5), 257–320, Oktober 1994 ISSN 0044-3468 C 21274 F

EITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde

Verlag Paul Parey Hamburg

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Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologiezentrum der Christian-Albrechts-Universität, Am Botanischen Garten 9, D-24118 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

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Fortsetzung 3. Umschlagseite

 Verlag: Paul Parey GmbH & Co. KG, Hamburg. Anschrift: Spitalerstr. 12, D-20095 Hamburg, Bundesrepublik Deutschland.
Printed in Germany by Westholsteinische Verlagsdruckerei Boyens & Co., Heide/Holst.

Z. Säugetierkunde 59 (1994) 257–273

ISSN 0044-3468

Evolution, biogeography, and description of a new species of Fruit-eating bat, genus *Artibeus* Leach (1821), from Panamá

By Elisabeth K. V. Kalko and C. O. Handley, Jr.

Division of Mammals, National Museum of Natural History, Smithsonian Institution, Washington, USA and Smithsonian Tropical Research Institute, Balboa, Republic of Panama

Receipt of Ms. 15. 3. 1993
Acceptance of Ms. 6. 6. 1994

Abstract

We describe and name a new species of Neotropical fruit-eating bat, genus *Artibeus.* It is a local endemic, found only on Isla Escudo de Veraguas, approximately 18 km off the Caribbean coast of the province of Bocas del Toro in northwestern Panamá. Based on a variety of shared characters we assume that this new species has evolved from a species also ancestral to *Artibeus watsoni,* which is widespread and abundant on the mainland and other islands of Bocas del Toro. The new species is 15 % larger in mass than its mainland relative, 10 % larger in body dimensions, and 6 % larger in cranial dimensions. Several discrete morphological characters, particularly in the dentition, also distinguish this bat from *A. watsoni.* We discuss aspects of evolution and biogeography of *A. incomitatus* to elucidate factors which might have facilitated its speciation.

Introduction

Laguna de Chiriquí on the Caribbean coast of northwestern Panamá (province of Bocas del Toro, 30 km southeast of the Costa Rican boundary) harbors numerous islands (Fig. 1), all formed by rising sea level. The islands are small (the largest is only 59 km^2), are close to the mainland, and with one exception they lie in shallow water. Isla Escudo de Veraguas (hereafter, "Escudo"), is the exception. It is surrounded by deeper water and is relatively remote, approximately 18 km off the coast of the mainland and 50 km from the nearest of the other Bocas islands.

Most of the islands, except the smallest, are to some degree inhabited by people. Originally, all of the islands with dry ground were covered with evergreen forest. In recent centuries, repeated disturbance by humans has caused the extirpation of some of the fauna and has removed part or all of the old (primary) forest from most of the islands.

There has been surprisingly little interest in biological exploration of these islands. Wetmore in 1958, Handley in 1960, 1962, and 1963, and Daly and Myers in 1967 made brief forays to the islands. Recently, a group from the Smithsonian Institution initiated inventories and in-depth studies of the island ecosystems. Its annual expeditions from 1987–93 have touched all of the major islands and some points on the adjacent mainland, and made collections that include mammals, birds, reptiles, amphibians, and plants.

Like other systems of small islands, the Bocas islands have depauperate faunas and floras. Although most of the islands are very close to the mainland, small in size, and young in origin, the inventories have revealed relict taxa and morphological differentiation of taxa between islands and mainland, as well as between the islands themselves (e.g., Handley 1959a). This is of special interest, as it raises an essential question: Why is there large scale response to small scale isolation? Comparative studies of species assemblages occurring on the mainland and on the islands will reveal part of the answer. Here we describe a new species of bat, genus *Artibeus*, which is found only on Isla Escudo de Veraguas, Panamá.

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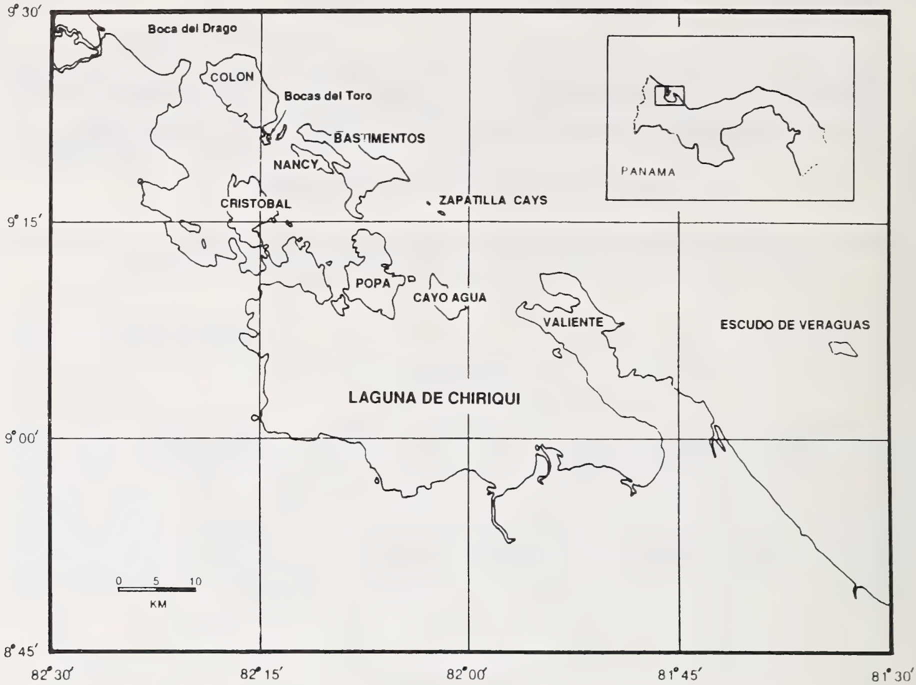

Fig. 1. Archipelago of Laguna de Chiriquí, Bocas del Toro, Panamá

Material and methods

Study area

Escudo is a small (4.3 km^2), triangular, heavily forested island in the Carribean, 17.6 km off the mainland Península Valiente. From a distance Escudo appears to be flat but, except for red mangrove (*Rhizophora*) swamps at eastern and western extremes, its surface is washboard-like. Its topography consists of a symmetrical series of low (< 50 m), steep-sided, flat-topped, parallel ridges separated by small, narrow swamps.

Escudo is the most remote of the Bocas islands. Merrill Varn and Charles Handley (unpubl. studies) have found it to be the oldest, formed by rising sea level. Varn and Handley correlated ocean floor topography around Escudo with dates from pollen and coral cores from the western Carribean (e.g., Bartlett and Barghoorn 1973). Their studies show that until sea level had risen to about 29 m below present sea level (about 9000 years before present, B. P.) Escudo was part of the mainland.

As sea level continued to rise, isolation of Escudo proceeded rapidly. Within 500 years (about 8500 years B. P.), at a sea level 25 m lower than present, the seaway between Escudo and the mainland had already opened to about 3 km. Within another 700 years (about 7200 years B. P.) sea level had risen to 15 m below present, and the distance between Escudo and the mainland had widened rapidly to about 12 km. Thereafter, the channel gained width gradually to its present 17.5 km.

Weather conditions

Frequent storms, accompanied by high winds and high tides, dominate the weather of Escudo. Distinct rainy seasons, June–August and November–December, are punctuated by indistinct dry seasons. Rainfall records have not been kept on Escudo, but because it is further away from the high mountains of the mainland, Escudo probably has less rain annually than the 2900 to 3200 mm recorded on the islands that lie within Laguna de Chiriquí.

Habitats

Evergreen forest covers about 95 % of Escudo. Less than 5 % of the island is currently cleared for houses, garden plots, plantains, and coconuts. Much of the forest is old growth, but tall young forest reveals that the western end of the island was extensively cleared in the recent past. All of the forest has been much damaged by wind, forming a peculiar natural mosaic of old and young growth.

Collections

Handley and F. M. Greenwell explored the southwestern sector of Escudo 19–24 March 1962, and collected among other mammals two species of bats, *Glossophaga soricina* (a nectar-feeder/insectivore) and specimens of a small canopy-foraging fruit bat resembling *Artibeus watsoni,* but larger. Again in 1990 (29 March–2 April), Handley and Greenwell surveyed the eastern quarter of Escudo. They mist netted many of the *Artibeus watsoni*-like bats and to the known chiropteran fauna they added a short-tailed fruit bat, *Carollia brevicauda,* which feeds on the fruits of shrubs.

During the last two weeks of March 1991, from a camp with indigenous people on the west shore, Handley and Penny Nelson collected bats in the western third of Escudo. They extended the series of *Artibeus watsoni*-like bats and added three more species of bats to the known fauna: *Saccopteryx leptura* and *Myotis riparius,* both insectivorous and feeding on the wing, and another small insectivorous bat, *Micronycteris megalotis,* which mainly gleans insect prey from surfaces. In April 1993 Kalko and Handley stayed in a camp of native fishermen on the northeastern shore of Esucodo to net and photograph the *Artibeus watsoni*-like bat. To date the native mammalian fauna of Escudo is known to include six species of bats, a marsupial, a sloth, and one rodent. In addition there are feral introduced house rats, house cats, and swine.

Specimens examined

Artibeus (new species), total 61. Panamá, Bocas del Toro: Isla Escudo de Veraguas (61).

Artibeus watsoni, total 134. Panamá, Bocas del Toro: Cayo Agua (12); Cayo Nancy (14); Cayo Zapatilla Este (3); Isla Bastimentos, Punta Vieja (9); Isla Colón, La Gruta (7); Isla Popa, 1 km SE Canal de Isla Deer (11); Isla San Cristóbal, Bocatorito (21); Península Valiente (various localities around the shores of Bahía Azul) (13); Tierra Oscura, 3.5 km S Cayo Tigre (8). Panamá, Chiriquí: Progresso, 1.6 km SW, 12.8 km SE, and 24.2 km SE (34); Puerto Armuelles, 3.2 km SW (2). Specimens representative of each taxon from each locality have been returned to Panamá. All specimens mentioned in the text are in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC.

Morphometrics

External and cranial dimensions were measured in millimeters; mass in grams. Total length, ear, wingspan, and mass were measured on fresh specimens in the field. Forearm, hind foot, tibia, and calcar were measured on dry skins of prepared specimens. External measurements were taken in the conventional manner (Handley 1988). Cranial measurements (Fig. 2) were taken as follows (a redefinition of the measurements first described in Handley [1959b], and subsequently widely used as a standard for bats):

Greatest length: Distance between the anteriormost point of the premaxillae and the hindmost point of the skull.

Zygomatic breadth: Greatest breadth between the outer edges of the zygomata.

Postorbital breadth: Least breadth across the constriction of the frontals, posterior to the postorbital processes or bulges.

Braincase breadth: Greatest breadth of the globular part of the braincase; measured by closing the calipers on the outer walls of the braincase and sliding down to the point of abrupt flare to the squamosal edge.

Braincase depth: Greatest distance between the medio-ventral surface of the basioccipital and the dorsalmost point of the braincase, the sagittal crest not included.

Maxillary toothrow length: Greatest crown length from the anteriormost edge of the canine to the posteriormost edge of the last molar in a maxillary toothrow.

Postpalatal length: Distance between the anteriormost point of the mesopterygoid fossa (disregarding a median projection) and the anteriormost point of the foramen magnum.

Maxillary breadth: Greatest alveolar breadth between the outer edges of the maxillary toothrows.

Canine breadth: Greatest distance between outer sides of upper canines at the alveoli.

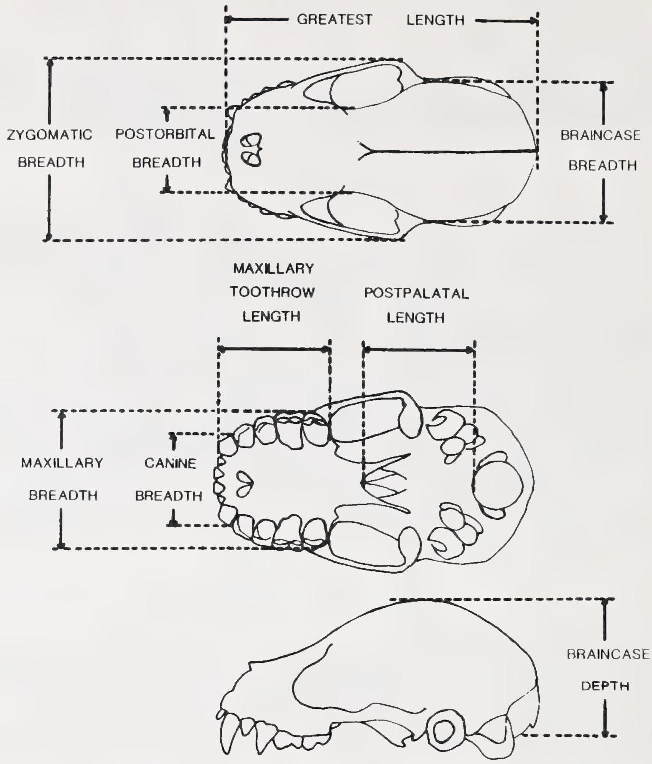

Fig. 2. Dorsal, ventral, and lateral views of a skull of *A. incomitatus*, illustrating method of taking cranial measurements

Only measurements of adults, recognized by closure of epiphyses, are included in our tabulations. As no sexual dimorphism was found, the data sets of both sexes were pooled. For mass, only males were used, as mass is variable in females.

External and cranial measurements taken in the laboratory were made with dial calipers to the nearest 0.1 mm. Data are presented as mean, ± two standard errors. They are rounded to the nearest 1/10 for the mean and to the nearest 1/100 for the standard error. The significance of differences in measurements between the new species and the related *A. watsoni* was verified by means of the Mann-Whitney U-test. Bivariate graphs were used to compare proportions of external and cranial features of both species. Next, we assessed the morphomentric variability of the specimens by examining them in multivariate space. Specifically, a Principal Components Analysis (PCA) was run, using the 15 variables listed in table 2. The Factors module of the program Systat for Windows (version 5.03; Wilkinson et al. 1992) was used for the analyses. The PCA (not rotated) was performed on a correlation matrix calculated with standardized data. To maximize the number of specimens used in the calculations, missing data were handled in a pairwise manner. That is, specimens with missing data were not automatically excluded because of a small amount of missing data during the calculation of the correlation matrix. For further discussion of the methods see Wilkinson et al. (1992), Davis (1986), and Chapman et al. (1981).

Results

Artibeus incomitatus, new species

Holotype

USNM 579125, adult male (testis 7×5 mm), skin and skull, collected 19 March 1991 by Charles Handley a meter or so above sea level, near West Point, Isla Escudo de

Veraguas, Bocas del Toro, Panamá, in a mist net in a clean coconut palm plantation. Original number, COH 17002.

Etymology

Latin, *incomitatus*, unaccompanied, alone; referring to the isolation of this bat on Isla Escudo de Veraguas, where it seems to be the only *Artibeus* and indeed the only stenodermatine.

Distribution

This bat is known only from Isla Escudo de Veraguas, province of Bocas del Toro, Panamá, where it is the most frequently netted bat. It was found in all habitats sampled, including upland forest, swamp forest, and coconut plantations. Elevational range, near sea level to 50 m, the highest point on the island.

Diagnosis

Artibeus incomitatus is characterized by large size; long, shaggy, bicolored dorsal fur; sooty dorsum; rather dark underparts; ill-defined facial stripes; cream-color on edges of ear, tragus and horseshoe; hairy posterior extremities; robust skull; broad, deeply-arched rostrum; supraorbital swelling not breaking supraorbital outline; capsulelike swellings on orbital wall always five, distinct, and subequal; subparallel zygomata; U-shaped anterior margin of mesopterygoid fossa; ill-defined inner edge of pterygoid fossa; equal or subequal cusps on I1; notches on hind edge of P4 few and indistinct; distance between paracone and protocone greater than distance between paracone and metacone on M1; paraconid cusp of m2 large, high, and situated on medial anterior edge of tooth; metaconid cusp of m2 inset from lingual margin; conulid between metaconid and entoconid of m2 large; m3 variably present or absent.

Description

Size large (forearm $\bar{x}$ = 42.7 mm, wingspread $\bar{x}$ = 327.0 mm, male mass $\bar{x}$ = 13.0 g). Dorsum varying from sooty to brown, average near Burnt Umber (capitalized color terms are from Ridgway 1912); underparts paler, near Warm Sepia; facial stripes usually poorly defined, whitish, but sometimes well defined, white; face, between stripes, black; membranes, ears, and noseleaf blackish; ear, tragus, and sometimes horseshoe of noseleaf narrowly edged with cream; lower edge of horseshoe free; wing attached to side of metatarsus; tibia, foot, and interfemoral membrane usually appear hairy.

Skull large (greatest length $\bar{x}$ = 20.9 mm, maxillary toothrow $\bar{x}$ = 7.0 mm); rostrum broad, deep, and arched, with prominent supraorbital swelling which does not break supraorbital outline; preorbital-supraorbital rim sharp-edged but low, disappearing before reaching ill-defined postorbital process; frontal wall of orbit rippled with the outlines of five well-defined, oblong, subequal capsules; postorbital constriction scarcely narrower than distance between postorbital processes; braincase narrow and deep, with evenly convex dorsal profile and low, sharp-edged sagittal crest, only vaguely connected anteriorly to postorbital processes; lambdoidal crest low and ill-defined in spots; zygomata weak and subparallel; palate wide, subcircular, with well-marked lateral depressions between canine and M1; postpalatal extension parallel-sided, with U-shaped posterior margin; pterygoid fossa with ill-defined inner edge, opening diagonally inward; basial pits (interauricular depressions) deep and well-defined, with rounded median septum; auditory bullae small.

Tooth formula I 2/2, C 1/1, P 2/2, M 2/2-3 X 2 = 28–30. I1 with equal or subequal cusps; notches on hind edge of blade of P4 usually few and indistinct; M1 wide, with both protocone and hypocone expanded and distance between paracone and protocone consid-

erably greater than distance between paracone and metacone; lingual longitudinal sulcus on p4 deep, extending to near base of tooth; anterolingual (paraconid) cusp of m2 large and displaced medially from lingual margin of tooth to form, with the anterolabial (protoconid) cusp, an anterior rim for the tooth (see Fig. 3 for nomenclature of cusps); conulid between metaconid and entoconid somewhat enlarged; m3 tiny, often lacking from one or both mandibles.

Measurements of the holotype

Adult male: Total length 59 mm, tail vertebrae 0 mm, hind foot (dry) 11 mm, ear from notch 17 mm, forearm 42.4 mm, wingspread 325 mm, tibia 15.2 mm, calcar 4.2 mm, mass 12.5 g. Greatest length of skull 20.6 mm, zygomatic breadth 11.7 mm, postorbital breadth 5.1 mm, braincase breadth 8.8 mm, braincase depth 7.7 mm, maxillary toothrow length 7.1 mm, postpalatal length 6.8 mm, maxillary breadth 8.5 mm, canine breadth 5.5 mm. See table 1 for a summary of measurements of a series.

Comparisons with related species

Compared with its close relative, *A. watsoni* of the Bocas islands and mainland, *A. incomitatus* averages 15 % greater in mass, 10 % larger in external dimensions, and 6 % larger in cranial dimensions. Every measurement except braincase depth is significantly

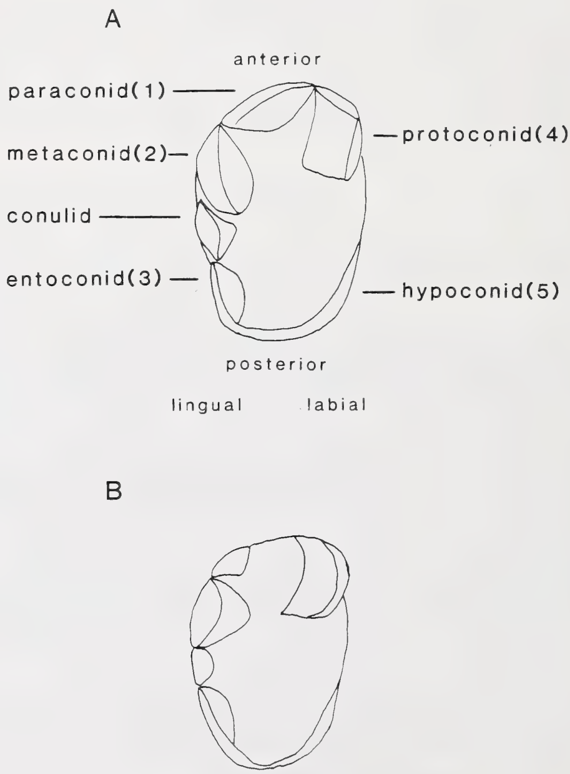

Fig. 3. Occlusal view of lower second molar (schematic drawings based on camera lucida sketches). A: *A. incomitatus* from Isla Escudo de Veraguas. B: *A. watsoni* of Península Valiente. Names of cusps are from Handley (1959b); numbers of cusps are from Andersen (1908)

larger in *A. incomitatus* ($p < 0.001$, Mann-Whitney U-test). Relative to *A. watsoni,* the largest measurements are tibia and calcar; the smallest are hind foot, zygomatic breadth, braincase breadth, and braincase depth. Bivariate scatter graphs of all individuals measured illustrate very well the high degree of separation between the two taxa. Figure 4 shows a pair of external characters; figure 5, cranial characters.

Further, the Principal Components Analysis (PCA) confirmed the large size difference between *A. incomitatus* and *A. watsoni.* The results of the PCA are summarized in tables 2 and 3, and figures 6 and 7. Fifteen components (PCs) were derived but only the first two axes had eigenvalues greater than 1; i.e. they represent more variance than any single variable.

PC-I accounted for almost 59 % of the variation in the data and is a classic size axis, indicated by the high positive loadings of all the variables (Tab. 2). This is very frequently the case in morphometric studies on single or closely related taxa (see Chapman et al. 1981). The loadings also indicate that of the original variables, greatest length is the best indicator of overall size (loading = 0.95) and braincase depth and postpalatal length are the least effective (both with loadings of approx. 0.55). The scores for the specimens (sample averages in table 3; scores plotted figures 6 and 7) give an indication of the overall size of the specimens, based on input from all 15 variables. A specimen with a high positive value for PC-I is very large compared to those with values near zero. Those with high negative values are the smallest (see Chapman et al. 1981).

PC-II accounted for just over 8 % of the variance in the data matrix and represents shape variation in braincase size (positive; braincase breadth and depth and ear versus selected standard lengths) (negative; total length, hindfoot, postpalatal length, tibia, and calcar). Not surprisingly, these variables tested to have the smallest loadings on PC-I. A specimen with a high positive value on this axis has a relatively large braincase and ear measurement and is relatively smaller in the length measurements. A high negative value would indicate the opposite.

In order to interpret these results we examined the scores; that is, how the specimens related to the new axes; and analyzed patterns in them relative to sex, taxon, and sample. No apparent trends could be discerned related to sex on either axis, suggesting that sexual dimorphism is not significant in these taxa.

Plotting the scores with the data coded to represent the specimens of each population (PC-I) indicate clear differences between *A. watsoni* and *A. incomitatus.* In PC-I, the specimens from Isla Escudo all plot positive, some highly positive, with relatively little overlap with the other samples (Fig. 6). This reflects the large size difference described for *A. incomitatus* relative to the much smaller *A. watsoni.* Plotting the average scores for each population shows trends for PC-II which are more subtle but still apparent (Fig. 7). Ignoring the Isla Escudo specimens and concentrating on *A. watsoni* alone, we see a mainland-island trend in the average values for PC-II. The Chriquí specimens not only tend to be small but they tend to have larger negative values for PC-II, indicating that they have relatively high values for the length measurements and small values for the braincase and ear measurements. On the other side of the PC-II trend are the larger near-shore islands of Colón and Bastimentos. Most other islands and Península Valiente are intermediate but closer to the larger islands. Isla San Cristóbal and Tierra Oscura, on the adjacent mainland, plot more toward the middle area. This suggests a northeast (island) – southwest (mainland) cline.

Dorsal coloration is similar in *A. incomitatus* and *A. watsoni,* but underparts are darker, gray-brown rather than buffy, in *A. incomitatus* (12 of 13 Península Valiente specimens are paler than the average Escudo specimen; only 6 of 45 Escudo specimens are as pale as the average Valiente specimen). Less than half (44 %) of Escudo specimens have prominent well-defined, white facial stripes, while more than two-thirds (69 %) of Valiente *A. watsoni* have prominent stripes. *A. incomitatus* usually (75 %) appears to have posterior

Table 1. **Measurements of adult *Artibeus***

Except for mass, which is for males only, measurements are for females and males combined. Each

Total length (mm)	Hind foot (dry) (mm)	Ear (mm)	Forearm (mm)	Tibia (mm)	Calcar (mm)	Wingspan (mm)	Mass (g)
Artibeus incomitatus, Isla Escudo de Veraguas							
59.7±0.61	11.1±0.16	17.7±0.14	42.7±0.30	14.7±0.15	5.0±0.13	327.0±2.30	13.0±0.34
55–64	10–13	17–19	40.6–44.4	13.6–15.8	4.0–5.9	305–343	10.8–16.0
(60)	(49)	(60)	(48)	(48)	(48)	(57)	(50)
Artibeus watsoni, Península Valiente							
53.7±2.1	10.1±0.26	16.6±0.46	38.4±0.8	13.3±0.38	4.2±0.16	298.3±5.44	10.9±0.72
46–60	9–11	15–18	35.9–40.7	12.4–14.7	3.4–4.5	282–310	9.5–13.0
(13)	(13)	(13)	(13)	(13)	(13)	(13)	(19)
Artibeus watsoni, Cayo Nancy							
54.1±0.96	10.6±0.26	16.1±0.51	38.0±0.58	13.3±0.50	4.4±0.20	294.6±6.00	11.3±0.62
52–59	10–11	14–17	35.9–39.2	12.2–14.9	3.8–5.1	277–315	9.5–13.0
(14)	(14)	(14)	(14)	(14)	(14)	(14)	(10)
Artibeus watsoni, all islands (except Escudo) and mainland							
54.5±0.65	10.4±0.10	16.0±0.25	38.5±0.25	13.0±0.14	4.4±0.07	296.6±2.10	11.1±0.27
42–60	9–12	12–18	35.9–41.6	11.3–14.9	3.4–5.4	273–317	9.0–14.0
(96)	(98)	(97)	(98)	(98)	(96)	(96)	(77)

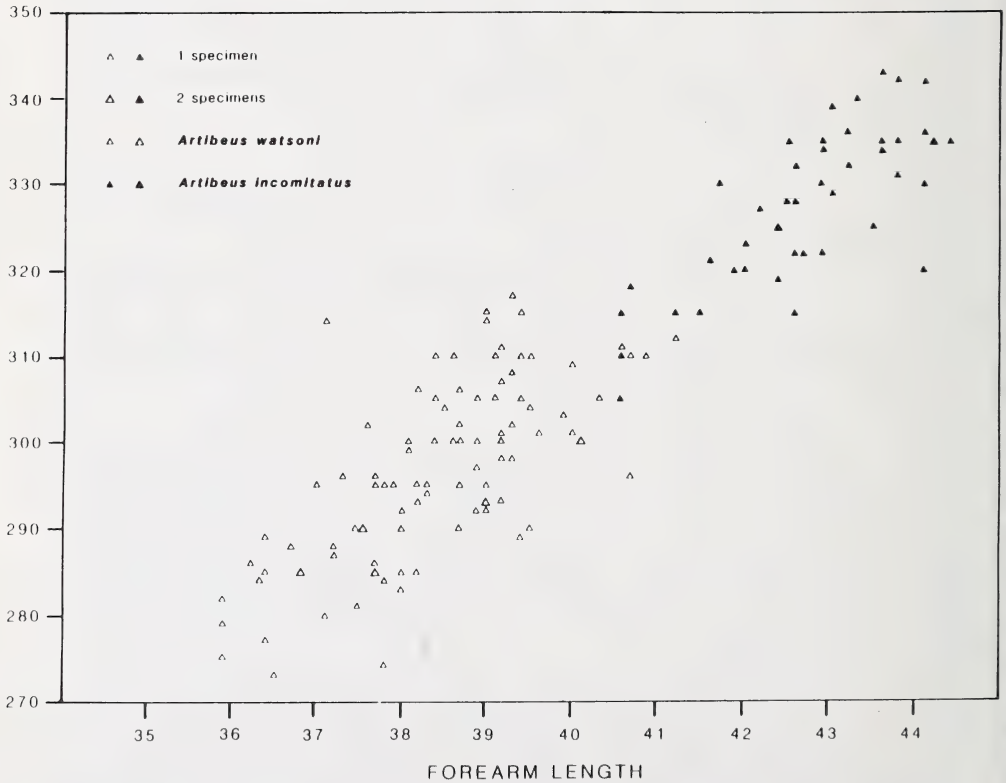

Fig. 4. Comparison of wingspread and forearm length in 45 specimens of *A. incomitatus* from Isla Escudo de Veraguas and 96 specimens of *A. watsoni* from shores and islands of Laguna de Chiriquí

incomitatus* and *A. watsoni

measurment is given as the mean ± 2 standard errors, Min/Max and the number of specimens measured

Greatest length (mm)	Zygomatic breadth (mm)	Postorbital breadth (mm)	Braincase breadth (mm)	Braincase depth (mm)	Maxillary toothrow (mm)	Postpalatal length (mm)	Maxillary breadth (mm)	Canine breadth (mm)
20.9±0.10 20.0–21.7 (60)	12.1±0.07 11.3–12.8 (58)	5.0±0.04 4.7–5.3 (60)	9.2±0.05 8.8–9.6 (60)	7.6±0.06 7.1–8.1 (59)	7.0±0.04 6.7–7.4 (60)	6.8±0.06 6.3–7.3 (57)	8.6±0.6 8.0–9.2 (60)	5.6±0.04 5.3–5.9 (60)
19.7±0.27 19.1–20.6 (13)	11.4±0.25 10.6–12.4 (13)	4.8±0.10 4.4–5.1 (13)	8.8±0.11 8.5–9.2 (13)	7.6±0.11 7.1–8.0 (13)	6.5±0.13 6.2–6.9 (13)	6.4±0.13 6.0–7.0 (13)	8.1±0.17 7.6–8.8 (13)	5.2±0.10 4.9–5.5 (13)
19.5±0.19 19.1–20.1 (11)	11.6±0.17 11.1–12.4 (13)	4.7±0.06 4.5–4.9 (13)	8.9±0.13 8.4–9.3 (13)	7.5±0.13 7.1–7.8 (10)	6.5±0.09 6.1–6.7 (13)	6.3±0.10 6.1–6.7 (11)	8.0±0.17 7.4–8.4 (12)	5.2±0.12 4.8–5.5 (12)
19.6±0.08 18.7–20.6 (94)	11.6±0.07 10.6–12.4 (91)	4.7±0.03 4.3–5.1 (96)	8.8±0.04 8.3–9.3 (96)	7.5±0.05 7.0–8.2 (93)	6.5±0.04 6.1–6.9 (97)	6.4±0.05 5.9–7.2 (93)	8.1±0.05 7.4–8.8 (95)	5.3±0.04 4.8–5.7 (95)

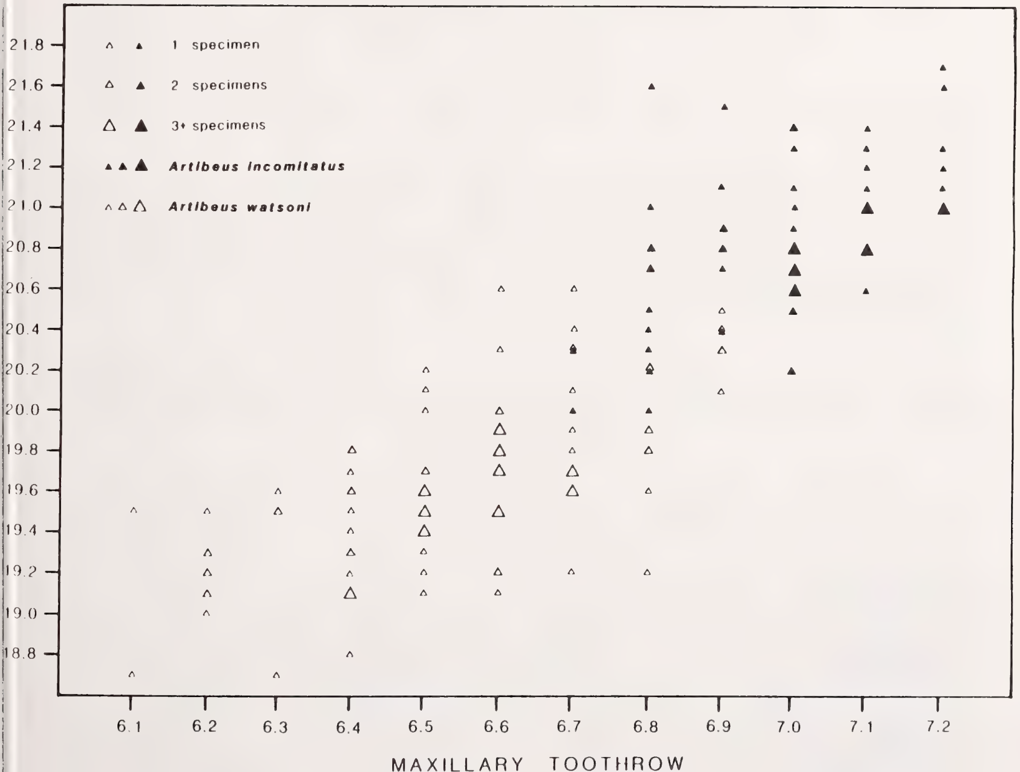

Fig. 5. Comparison of greatest length of skull and maxillary toothrow length in 60 specimens of *A. incomitatus* from Isla Escudo de Veraguas and 94 specimens of *A. watsoni* from shores and islands of Laguna de Chiriquí

Table 2. **Variables used in Principal Components Analysis and their loadings for the first two Principal Components**

Eigenvalues and percent variance explained for first two Principal Components, are also tabulated

Variables	Loadings PC-I	PC-II
Total length	0.6674	−0.4435
Hind foot	0.6288	−0.3199
Ear	0.7035	0.2067
Forearm	0.8839	−0.1481
Greatest length	0.9499	0.0583
Zygomatic breadth	0.8525	0.1941
Postorbital breadth	0.7235	−0.0401
Braincase breadth	0.8155	0.3313
Braincase depth	0.5509	0.6081
Maxillary toothrow	0.8946	0.1222
Postpalatal length	0.5485	−0.3666
Maxillary breadth	0.8696	0.1430
Canine breadth	0.8351	0.0499
Tibia	0.8050	−0.2376
Calcar	0.6107	−0.3233
Eigenvalue (Total = 15)	8.8138	1.2193
1 % Variance explained	58.7589	8.1287

extremities (tibia, foot, and interfemoral membrane) hairy, whereas *A. watsoni* appears to have these parts almost naked (12 of 13 specimens from Península Valiente). Under magnification all specimens of both species prove to have hairy posterior extremities. Hairs are longer and possibly denser in *A. incomitatus*.

The skull of *A. incomitatus* is heavier and more bulky than the skull of *A. watsoni.* Supraorbital swelling is pronounced, but usually not sufficiently in Escudo specimens (23 of 30) to break the smooth-edged supraorbital outline, whereas only 11 of 30 *A. watsoni* have the outline unbroken. Capsule-like swellings on the frontal wall of the orbit always five, distinct, and subequal in *A. incomitatus,* sometimes only four, often indistinct, and always variable in size in *A. watsoni.* Zygomata usually subparallel (18 of 30) in Escudo specimens, but almost always (26 of 30) narrow anteriorly and swept-back in *A. watsoni.* Anterior margin of mesopterygoid fossa almost always (26 of 30) U-shaped in *A. incomitatus*, often V-shaped in *A. watsoni* (17 of 30). Inner edge of pterygoid fosa always ridged in *A. watsoni*, but ridge almost always (26 of 30) ill-defined or absent in *A. incomitatus*.

Cusps of I1 almost always (39 of 42) equal or subequal in *A. incomitatus*, while the outer cusp usually (30 of 44) is larger in *A. watsoni.* Notches on the hind edge of the blade of P4 usually few and indistinct in Escudo specimens (29 % with one sharp notch, 62 % with 1–3 obscure notches, and 9 % notchless), whereas 56 % of Valiente specimens have 1–3 sharp notches and 44 % have 1–3 obscure notches. The paraconid cusp of m2 has a medial location on the anterior edge of the tooth in 29 of 35 specimens of *A. incomitatus*, a

Table 3. **Statistics for scores from Principal Components Analysis of samples of *Artibeus incomitatus* from Isla Escudo de Veraguas and *A. watsoni* from ten localities in Bocas del Toro and Chiriquí, Panamá**

Localities	Abbrev. for Locality	N	Factor Score Data PC-I Mean/S.E.	PC-II Mean/S.E.
Isla Escudo	E	45	1.31/0.07	−0.43/0.14
Península Valiente	V	13	−0.47/0.19	0.88/0.19
Isla Colón	C	4	−0.03/0.62	1.21/0.19
Isla Bastimentos	B	8	−0.54/0.21	1.30/0.35
Cayo Nancy	N	9	−0.44/0.18	0.27/0.29
Cayo Zapatilla Este	Z	3	−0.51/0.43	0.79/0.40
Cayo Agua	A	11	−0.78/0.13	0.36/0.26
Isla Popa	P	11	−0.32/0.09	0.22/0.22
Isla San Christóbal	S	16	−0.30/0.10	0.08/0.18
Tierra Oscura	T	7	−0.56/0.14	−0.21/0.23
Progresso, Chiriquí	Q	13	−0.98/0.09	−1.00/0.17

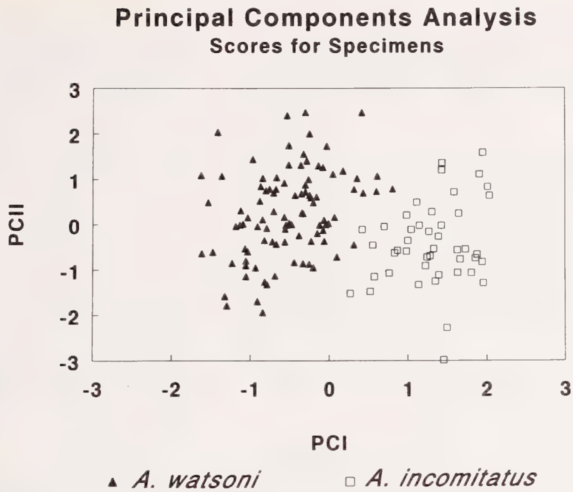

Fig. 6. Results of Principal Components Analysis. Scores of specimens plotted for PC-I (X-axis) versus PC-II. Labels indicate species of specimen; triangle = *Artibeus watsoni*; square = *Artibeus incomitatus*

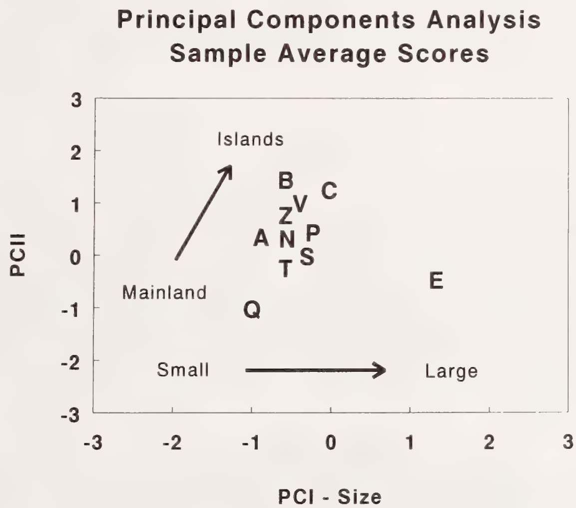

Fig. 7. Results of Principal Components Analysis. Scores of specimens plotted for PC-I (X-axis) versus PC-II. Labels are mean values for populations (see Tab. 3)

lateral location in 45 of 46 specimens of *A. watsoni* (Fig. 2). This cusp is large (24 of 35) and high (18 of 35) in *A. incomitatus*, but small (42 of 46) and low (34 of 46) in *A. watsoni*. The metaconid cusp of m2 is inset from the lingual margin of the tooth in 22 of 35 specimens from Escudo, but is on the margin of the tooth in 41 of 46 *A. watsoni*. The conulid between the metaconid and entoconid cusps of m2 is large in 28 of 35 *A. incomitatus*, but in only 13 of 46 *A. watsoni*. Presence or absence of m3 on either mandible varies among populations of these bats, from a frequency of zero on Cayo Zapatilla Este and 0.5 on Cayo Nancy to 1.7 on Isla Popa and 2.0 on Isla Colón. The mean for Isla Escudo is 1.2 and the mean for the other islands and mainland of Bocas del Toro collectively is 1.5.

There is another small species of *Artibeus* (*A. phaeotis*), on the mainland and on some of the islands of Bocas del Toro. Compared with *A. incomitatus*, it is smaller, in the size range of *A. watsoni*; dorsal fur distinctly tricolor versus bicolor or indistinctly tricolor, shorter (6 mm versus 8 mm), smooth-lying rather than shaggy, and brownish rather than sooty; underparts more buffy; facial stripes pure white and sharply defined; margins of ears, tragus, and sometimes noseleaf yellow or orange rather than creamcolor. Rostrum shorter, shallower, flatter, and less arched; supraorbital not swollen; postorbital constriction narrower; braincase deeper and wider; zygomata taper (narrow anteriorly, flaring posteriorly); palate shorter and broader, subcircular; lateral palatal depressions usually ill-defined or absent; anterior edge of mesopterygoid fossa V-shaped; inner edge of pterygoid fossa sharply ridged, constricting roof of mesopterygoid fossa, and causing pterygoid fossa to open posteriorly rather than inward. Protocone of M1 relatively closer to metacone, so that protocone, metacone, and paracone usually come close to forming an equilateral triangle; m2 longer and narrower, but otherwise like m2 of *A. watsoni*; m3 always absent.

Remarks

To check for the possibility that *A. watsoni* as well as *A. incomitatus* might occur on Escudo, during the 1991 expedition to Escudo Handley selectively collected the smallest *Artibeus* that were netted. This skewed the *A. incomitatus* series toward the small side, but did not turn up any specimens in the size range or with morphological characters of *A. watsoni*. Actually, there is surprisingly little variation, considering the size of the series (159 specimens), among the skulls from Escudo on the one hand and those from all other islands and mainland on the other (Tab. 1; Figs. 4, 5).

Ectoparasites

Parasitic flies (Streblidae) collected by Handley and Nelson from *A. incomitatus* on Isla Escudo prove to represent a well-differentiated undescribed species, apparently evolved from *Paratrichobius lowei* Wenzel, a parasite of *A. watsoni* (R. V. Peterson, unpubl. results). *P. lowei* has been reported from *A. watsoni* taken in eastern Panamá (San Blas and Darién) (Wenzel et al. 1966) and from "*Artibeus cinereus*" taken in Venezuela (Bolívar) (Wenzel 1976). The Venezuelan hosts have been reidentified as *Artibeus glaucus bogotensis*, a member of the *A. glaucus* group, which also includes *A. watsoni* (Handley 1987).

Discussion

Taxonomic status of *A. incomitatus*

Insular populations of organisms showing morphological differentiation from mainland taxa pose taxonomic problems in interpreting the observed variability. As summarized by Wilson (1991), differentiated island populations can depending on the conceptual viewpoint of the researcher be regarded either as subspecies of mainland species or as endemic island species.

Because geographic isolation interrupts or diminishes gene flow between populations, it represents one of the most important factors promoting speciation. However, assessing whether spatial isolation on an island has been sufficient to produce reproductive isolation, the basic criterion of the biological species concept, remains an imponderable problem always confounding systematic studies of island organisms. Often this question can be addressed only indirectly.

Ideally, information about formation of the island, degree and duration of isolation

from the mainland, detailed studies on morphological and genetic variability of island and mainland populations, as well as studies of ecological (e.g., community structure), behavioral, and physiological characteristics should be available to allow a taxonomist to judge adequately the significance of observed differences between island and mainland populations. In reality such information seldom is available.

In our study we have described *A. incomitatus* as a species endemic on Isla Escudo de Veraguas, Panamá. We compared it with a similar species, *A. watsoni*, which is widespread on the mainland from southern México to Ecuador (Hall 1981). Based on a set of morphological characteristics shared by the two taxa we assume that *A. incomitatus* and *A. watsoni* have evolved from a common ancestor. We further assume that the characters which distinguish *A. incomitatus* and *A. watsoni* were variable in the ancestral bat before Isla Escudo de Verguas was isolated. After isolation the characters were variously accentuated in the evolving *A. incomitatus* and *A. watsoni*.

For several reasons we regard *A. incomitatus* and *A. watsoni* as species rather than as subspecies. First, there is the matter of scale, a commonly used criterion for ranking insular populations. If differentiation of the organism on an island is greater than differentiation between contiguous populations on the mainland which are supposed to be geographic variants, then the insular population should be regarded as a species. *A. watsoni* is regarded as monotypic throughout its range (Hall 1981), but actually it is geographically variable (Handley 1987; unpubl. results). However, the degree of difference is much greater between the insular *A. incomitatus* and the mainland *A. watsoni* than between any of the mainland populations of *A. watsoni*. There is no evidence of intergradation between the taxa, and every external and cranial dimension we measured, except cranial breadth, is significantly larger in *A. incomitatus*.

Principal Components Analysis confirms the great size difference apparent in the Escudo specimens. It also indicates an interesting trend, from the mainland across the inner islands of Laguna de Chiriquí, in both shape and size of skull that invites further study, especially documentation of genetic relationships of the samples. The results could demonstrate a morpho-genetic cline, indicating a species in the process of spinning off from a sister species, or show the progressive fragmentation of a species-range, with the predictable effect of isolating various populations.

However, molecular analysis alone, which is increasingly used to determine phylogeny and taxonomic status of organisms, is not necessarily the solution to the species dilema. For example, recent studies on Peruvian *Sturnira* (Phyllostomidae) led to conflicting evidence in morphological and genetic characters (Pacheco and Patterson 1992). Some of the morphological characters did not show in the genetic analysis and, in reverse, some molecular differences did not show in morphology.

Second, in addition to statistical differences in external and cranial measurements, *A. incomitatus* and *A. watsoni* differ also in numerous discrete morphological characters in the dentition, cranium, and pelage. Among the dental characters that distinguish *A. incomitatus* the one we consider to be the most significant involves the size, shape, and location of cusps on the second lower molar. The placement of the paraconid in *A. incomitatus* on the anterior margin of the tooth, close to the protoconid, has the effect of giving the tooth a substantial anterior rim, undeveloped in *A. watsoni*. In contrast, *A. watsoni* almost always has a wide, low gap between the paraconid and the protoconid. These differences in dentition must give the teeth of the two species slightly different functional characteristics, which remain to be explained. The most distinctive cranial feature of the Escudo bat is suppression of the ridge at the inner edge of the pterygoid fossa. In pelage, *A. incomitatus* is characterized by drabness: sooty dorsal coloration, darkening of the underparts, and obsolescence of facial stripes, only to a limited extent seen in the mainland bat.

Third, the host-specific parasitic streblid fly of *A. incomitatus* has differentiated to the species level from the ancestral fly on *A. watsoni*. Assuming that the coevolution in host

and parasite proceeds at a similar rate this evidence also supports the specific status of *A. incomitatus*.

Fourth, long-term studies of *A. watsoni* in Isla Barro Colorado Island (BCI), a field station of the Smithsonian Tropical Research Institute, Panamá, suggest that this bat, and presumably also *A. incomitatus*, have very small home ranges, thus further enforcing the isolation of mainland and island populations. On this small (1500 ha, 5 × 5 km) island in Gatun Lake (Panamá Canal), 40 marked *A. watsoni* were recaptured up to three times during a five year interval. Most individuals (36) were recaptured within 1 km of their mark sites, more than 50 % of them (22) at the original mark site. The greatest recorded movement was only 3 km. The only movement over water probably was no more than 200 m. Furthermore, the wing morphology of *A. incomitatus* and *A. watsoni* makes it highly unlikely that either could commute between the mainland and Escudo. Both have rather short, broad wings typical of most stenodermatine bats. This wing shape adapts them for slow, maneuverable flight in and around vegetation but constrains them from sustained flight over long distances (Norberg and Rayner 1987). Moreover, the frequent storms around Escudo would further limit movement between mainland and island.

Evolution on Escudo

The isolation of Escudo limits immigration and facilitates evolution. Escudo is more isolated than any other island of Bocas del Toro. On it *A. incomitatus* has differentiated to the species level. On the other islands, which are much closer to the mainland, populations of *A. watsoni* are barely distinguishable from those of the mainland.

Seven of the nine species of native mammals of Escudo are differentiating from their mainland counterparts. *Artibeus incomitatus, Glossophaga soricina, Micronycteris megalotis,* and *Hoplomys gymnurus* are larger; *Caluromys derbianus, Carollia brevicauda,* and *Bradypus variegatus* are smaller. Only the aerial insectivorous bats, *Saccopterys leptura* and *Myotis riparius*, seem to be morphologically unchanged. Some of the birds of Escudo clearly are isolated and have undergone morphological differentiation. The hummingbird (*Amazilia handleyi*), manakin (*Manacus amitinus*), and wren (*Thryothorus nigricapillus*) are strikingly larger and more colourful than their mainland congeners, near the species level of differentiation. The blue tanager (*Thraupis episcopis*) is less differentiated and may be a later immigrant, or may be evolving more slowly. S. L. Olson (pers. comm.) has found the rail, kingfisher, pigeon, parrot, flycatchers, and warbler of Escudo to be little if any differentiated. Among the resident land birds, at least the pigeon and parrot may fly periodically to the mainland.

Escudo has existed at most only about 9000 years, but once established, the channel separating it from the mainland widened rapidly and the sedentary nature of the *Artibeus* insured its quick isolation from parental populations on the receding mainland. Although 9000 years appears to be little time for speciation there are other examples in mammals. Bergstrom and Hoffman (1991) have inferred for example that the most recent cycle of differentiation and speciation in chipmunks (*Tamias*) in the montane islands in the Great Basin and southern Rocky Mountains of the southwestern United States has occurred in the 10,000 years since the Pleistocene (see also Patterson 1982).

Factors leading to evolution and extinction on Escudo

We assume that all of the mammals of Escudo may be survivors of selective extinction from a species-rich mainland fauna following the fragmentation of Escudo. The inner islands, closer to the mainland, harbor more species. With increasing distance from the mainland the number of species declines. Extinction is rapid and extensive on small islands, leading

soon to diminished resource and habitat diversity and consequently to reduced faunal diversity.

Compared with their mainland counterparts, island populations of animals often undergo significant changes in body size. Smaller animals tend to increase in size whereas larger animals tend to decrease in size (e.g. CASE 1978; HEANEY 1978; LAWLOR 1982; LOMOLINO 1985). On the Bocas islands we have found both phenomena – dwarfism and gigantism. For example the agouti (*Dasyprocta*), long-nosed armadillo (*Dasypus*), and sloths (*Bradypus* and *Choloepus*) on the islands are smaller than their mainland congeners whereas some rodents (e.g., *Tylomys*) are larger (HANDLEY, unpubl. results). A number of hypotheses, including resource and habitat limitation, interspecific competition, and predator pressure, have been put forward to explain this pattern (for summaries see as examples ANGERBJÖRN 1985 and LOMOLINO 1985).

The factors we regard as most significant in this process on Escudo are reduction in habitat diversity and the resulting resource limitation. At first glance resource limitation would seem to contradict our observation that *A. incomitatus* is significantly larger, and has a much higher population density than its mainland counterpart, *A. watsoni*. However, whereas *A. incomitatus* is the only stenodermatine on Escudo, on the mainland and on all other islands of Bocas del Toro, *A. watsoni* and other small stenodermatines compete for fruit with larger species, often in graded series of size classes. The decrease in abundance and diversity of fruiting plants on islands is a particularly serious problem for frugivorous bats which live on a very tight energy budget and need a constant supply of fruits (HANDLEY et al. 1991; MORRISON 1980). First observations on Escudo indicate that there is insufficient food for larger bats. For example, there are few figs of any kind on Escudo, and *Ficus insipida* seems not to occur there. Throughout Panamá this species is a major food source for large numbers of fruit-eating bats ranging in mass from 8–75 g (e.g. BONACCORSO 1979; HANDLEY et al. 1991). We assume that release from interspecific competition with other frugivorous stenodermatines might have freed the evolving *A. incomitatus* to occupy a wider niche and thus to become bigger and more abundant. A larger body size would adapt it to utilize the full (although limited) range of fruit sizes available on Escudo. *A. incomitatus* may have already reached its potential maximum body size. Its size ratio of 1.17 to its mainland relative, *A. watsoni*, is comparable to means of ratios of large suits of pairs of island and mainland species compiled by LOMOLINO (1985).

Another factor pressing for larger size in *A. incomitatus* might be the reduced and seasonally variable abundance of fruit on Escudo. LINDSTEDT and BOYCE (1985) have argued that seasonality selects for larger body size, which enhances survivorship through increased fasting endurance. Larger bats tolerate hunger better than smaller bats do. Although frugivorous neotropical bats typically have little body fat (MCNAB 1976) we found substantial amounts of fat in *A. incomitatus* but little or none in *A. watsoni* collected at the same season.

WILSON (1991) found similar trends in size among small mammals on the Tres Marías islands of Mexico. These islands are further from the mainland and much larger than Escudo. As on Escudo, only one stenodermatine is present (*A. intermedius koopmani*). However, *Artibeus intermedius* already is one of the largest stenodermatines, yet the island bat is still larger than mainland *A. intermedius*. Furthermore, WILSON (1991) found higher diversity in insectivorous vespertilionid bats than in the mainly frugivorous and/or nectarivorous phyllostomids. He postulated that their lower diversity might reflect unpredictability of supplies of fruit and flowers.

Acknowledgements

More than to any other person we are indebted to LIGIA PAGET of Bocas del Toro for her unfailing support and friendship. We are grateful to FRANCIS M. GREENWELL and PENNY NELSON who helped

to collect and to prepare the specimens of *A. incomitatus*. The Instituto Nacional de Recursos Naturales Renovables of Panamá (INRENARE), notably Roberto Arrango, provided collecting and export permits. Mercedes Arroyo, Isis Ivancic, Gloria Maggiori, and María Morello of the Smithsonian Tropical Research Institute (STRI) expedited administrative and logistical details. We are most grateful to Arloine Hood and Kerry Thomson who processed the specimens in the museum; Merrill Varn for her reconstructions of prehistoric shorelines; Ralph Chapman for his invaluable generosity of sharing his expertise in statistics and morphometrics with us; and Darelyn Handley who prepared the table of measurements and edited the manuscript. The Escudo expeditions were financed by grants from the National Science Foundation and the National Museum of Natural History (Nelson Fund and Reseaerch Opportunities Fund), the Smithsonian Office of Products Development and Licensing, and a gift from James and Paula Nelson of Hillsboro, Oregon. E. K. V. Kalko was suported by a NATO postdoctoral fellowship. Transporation was furnished by the U.S. Army (Maj. Vernon J. Tipton), STRI (John Christy, Egbert Leigh and David West), United Brands, Changuinola Division (Cameron Forsythe, General Manager), and Asociación Nacional para la Conservación de la Naturaleza, Panamá (ANCON).

Zusammenfassung

Evolution, Biogeographie und Beschreibung einer neuen, fruchtfressenden Fledermausart der Gattung Artibeus Leach (1821) aus Panama

Wir beschreiben und benennen eine neue, fruchtfressende Fledermausart der Gattung *Artibeus* aus den Neotropen. Die neue Art ist ein Lokalendemit und kommt nur auf der Insel Escudo de Veraguas, Panamá, vor. Escudo de Veraguas liegt in der Provinz Bocas del Toro in Nordwest-Panamá, ungefähr 18 km von der karibischen Küste entfernt. Aufgrund einer Vielzahl gemeinsamer Merkmale nehmen wir an, daß sich die neue Art aus einer *Artibeus watsoni*-nahestehenden Fledermausart entwickelt hat. *A. watsoni* ist auf dem angrenzenden Festland und auf den anderen Inseln in der Provinz Bocas del Toro weitverbreitet und häufig. Im Vergleich zu *A. watsoni* wiegt die neue Art ca. 15 % mehr, die Körperproportionen sind um ca. 10 % und die Schädeldimensionen um ca. 6 % größer. Zudem unterscheidet sich die neue Art in einer Anzahl diskreter morphologischer Merkmale, insbesondere in der Bezahnung von *A. watsoni*. Wir diskutieren Aspekte zur Evolution und Biogeographie von *A. incomitatus* und leiten daraus Mechanismen ab, die möglicherweise zur Artbildung dieser neuen Fledermausart beigetragen haben.

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Authors' addresses: Dr. Elisabeth K. V. Kalko and Dr. Charles O. Handley, Jr., Division of Mammals, National Museum of Natural History, MRC-NHB 108, Smithsoninan Institution, Washington, DC 20560, USA, and Smithsonian Tropical Research Institute, P. O. Box 2072, Balboa, Republic of Panamá

Z. Säugetierkunde 59 (1994) 274–281

ISSN 0044-3468

Contribution to the knowledge of the bat fauna of Bioko island, Equatorial Guinea (Central Africa)

By J. Juste B. and C. Ibáñez

Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas, Sevilla, Spain

Receipt of Ms. 16. 3. 1994
Acceptance of Ms. 2. 6. 1994

Abstract

Although having been long studied, the bat fauna of Bioko island (formerly Fernando Poo, Equatorial Guinea, Central Africa), is still little known. The species *Hipposideros commersoni, Glauconycteris beatrix, Pipistrellus (P.) kuhlii, P. (N.) tenuipinnis,* and *P. (N.)* cf. *capensis* are reported for the first time. Furthermore, the species *Myonycteris torquata, Taphozous mauritianus, Nycteris arge, Hipposideros cyclops, Glauconycteris poensis, Mops (X.) spurrelli* and *M. (X.) thersites*, previously reported as doubtful, are confirmed on Bioko. These results increase the bat checklist for Bioko island by 25 %, and it now includes 26 species.

Introduction

Bioko island (formerly Fernando Poo), is situated 32 km off the coast of Cameroon (3° 48′ –3° 12′ N, 8° 25′ –8° 57′ E), in the middle of the Gulf of Guinea. Since it was a commonly used starting point for many scientific expeditions to the African mainland, many mammal species, including bats, were first described from Bioko specimens in the 19th century (e.g. *Dendrohyrax dorsalis, Colobus satanas, Glauconycteris poensis, Rhinolophus landeri,* etc.). Nevertheless, our understanding of the bat fauna of Bioko, is still fragmentary. Basilio (1962), in a general view of the fauna of Equatorial Guinea (a former Spanish colony), gave some data on Bioko's bats. Eisentraut (1964, 1973) summarized the bat fauna of Bioko after collecting on the island for some months. He considered that up to 20 species were present (in 1973); although he doubted some (e.g. *Myonycteris torquata* or *Glauconycteris poensis*) and stressed the need to confirm others. Later on, Ibáñez and Valverde (1985) added *Eptesicus platyops* (as a probable synonym of *E. serotinus*) to the bat list of Bioko.

Material and methods

From 1988 to 1991, a systematic sampling was carried out by the senior author throughout the island. Bats were caught by netting and visiting possible roosting places as part of a wider study of the bat fauna of the Gulf of Guinea Islands. Collected specimens were deposited in the Estación Biológica de Doñana (EBD) collections and were compared with material from the Museo Nacional de Ciencias Naturales de Madrid (MNCN). Selected measurements of adult specimens are given in mm, together with the number of specimens (brackets) and ranges (parentheses). Both sexes were summarized when no significant dimorphism was found.

Abbreviations used are: FA = forearm length; GSL = greatest skull length; CBL = condylobasal length; CCL = condylocanine length; ZW = zygomatic width; DCC = distance between canines (from outer side) and MW = mastoid width. Species are named according to Corbet and Hill (1986), except for Vespertilionidae, which follow Hill and Harrisonj (1987), and Molossidae, which follow Koopman (1993).

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Results

As a result of this research, five new species are recorded and another seven confirmed. The list of bat species known to occur in Bioko comprises now 26 species.

Pteropodidae

Myonycteris torquata (Dobson, 1878)

Material [1]: Eolá river, Patio Vivancos, Baney: 1 subadult ♂.
Selected measurements: FA 58.0; GSL 31.0; CBL 29.8; ZW 18.9.
Remarks: The only known specimen was reported by Krumbiegel (1942) without locality. Eisentraut (1964) did not catch any specimens on his expeditions and even doubted its presence. In his *Myonycteris* revision, Bergmans (1976) studied only the skin of Krumbiegel's specimen and raised the possibility that the bat belongs to *M. brachycephala*, an endemic from nearby São Tomé island (Bocage 1889).

The Baney specimen confirms the presence of *Myonycteris torquata* on Bioko island. It was netted in a secondary forest surrounded by agricultural crops and cocoa plantations. Although still subadult, the skull clearly shows the typical *M. torquata* shape, mainly in its wide post-dental palatum bone and weak "fascia temporalis" in the zygomatic arches. Furthermore, the specimen does not share any of the characteristic dental features described by Andersen (1912a) for *M. brachycephala*. *Myonycteris torquata* has not been found again, in spite of intense netting efforts. It can be considered the most rare fruit bat on Bioko island. Moreover, the fact that the species is subadult and was captured in the western point closest to the mainland would support the possibility of *M. torquata* being represented on Bioko only by vagrant or migrant individuals that sporadically reach the island.

Emballonuridae

Taphozous mauritianus Geoffroy, 1818

Material [13]: All obtained in Malabo: 6 adult ♂♂, 2 subadult ♂♂, 3 adult ♀♀ and 2 subadult ♀♀.
Selected measurements [9]: FA mean 61.2 (58.7–65.0); GSL mean 22.1 (21.8–22.5); CCL mean 20.6 (20.2–21.2); ZW mean 12.9 (12.4–13.4).
Remarks: *Taphozous mauritianus* was apparently first cited from Bioko as early as 1876 by Peters (Eisentraut 1964). Another specimen is mentioned by Basilio (1962), but Eisentraut did not find it. The presence of *T. mauritianus* is confirmed by our series. The bats were caught while roosting in coconut palms in Malabo city. Therefore, the species probably occupies most of the coastal coconut tree plantations on the island. The confirmation of this widespread African species was expected since it has been recently found on other islands in the Gulf of Guinea (Juste and Ibáñez 1993).

Nycteridae

Nycteris arge Thomas, 1903

Material [42]: Malabo–Riaba road, km 3: 1 adult ♂. Malabo–Riaba road, km 10: 1 adult ♂ and 2 adult ♀♀. Malabo–Riaba road, km 61: 6 adult ♂♂ and 7 adult ♀♀. Malabo–Riaba road, km 62: 2 adult ♂♂ and 3 adult ♀♀. Bantabaré, Riaba: 1 adult ♀. Malabo–Luba road, km 3: 1 adult ♂ and 3 adult ♀♀. Malabo–Luba road, km 13: 1 adult ♂ and 1 adult ♀. Malabo–Luba road, km 15: 1 adult ♀. Elgorriaga, Malabo–Luba road, km 19: 1 adult ♂.

Malabo–Luba road, km 40: 2 adult ♂♂. Malabo–Luba road, km 42: 2 adult ♂♂ and 2 adult ♀♀. Batete, Luba: 1 adult ♂. Luba: 4 adult ♂♂.
Selected measurements: FA [42] mean 42.1 (36.4–48); GSL [24] mean 19.5 (18.2–21.1); CCL [23] mean 16.9 (15.9–18.4); ZW [24] mean 11.4 (10.2–12.6); DCC [24] mean 4.7 (4.3–5.5).
Remarks: The only known specimen was obtained at the beginning of the century on the southwestern coast (Bantabaré) and recorded by Andersen (1912b) and considered as *N. hispida* (Eisentraut 1973). Our series confirms the presence of *N. arge* on Bioko island as a common species in both forest and cocoa plantations all over the island. It has been found inside tree holes and drains. The wide variation in the measurements of the population is outstandig; even so, our figures fit well within the ranges given for the species (Koopman 1975; Van Cakenberghe and De Vree 1985).

Hipposideridae

Hipposideros commersoni (Geoffroy, 1813)

Material [22]: Ericorico river, Malabo–Riaba road, km 3: 2 adult ♂♂, 1 subadult ♂. Grande river, Riaba: 1 adult ♀. Timbabé river, Malabo–Luba road, km 3: 1 adult ♂. Basupú, Malabo–Luba road, km 14: 1 adult ♀. Bosao river, Malabo–Luba road, km 20: 3 adult ♂♂ and 3 adult ♀♀. Apú river, Malabo–Luba road, km 21: 1 subadult ♂ and 1 subadult ♀. Eolá river, Patio Vivancos, Baney: 3 adult ♂♂, 1 subadult ♂, and 2 subadult ♀♀. Borabuopé river, Mallo plantation, Malabo: 2 adult ♂♂.
Selected measurements: Males: FA [12] mean 104.0 (102.0–105.8); GSL [11] mean 38.7 (36.1–39.2); CBL [11] mean 33.5 (31.3–34.7); DCC [11] mean 11.2 (10.5–11.8); ZW [11] mean 22.0 (21.4–23.2). Females FA [6] mean 99.0 (96.4–100.4); GSL [4] mean 37.2 (36.5–38.6); CBL [4] mean 32.4 (31.7–33.1); DCC [4] mean 10.3 (9.8–11.1); ZW [4] mean 20.6 (19.9–21.8).
Remarks: *Hipposideros commersoni* was first cited for Bioko by Cabrera (1912) by means of a purchased male specimen. It was not considered by Eisentraut (1964, 1973) and Hayman and Hill (1971) but was mentioned again in a recent inventory of the bat collection of the Museo de Ciencias Naturales in Madrid (Ibáñez and Fernández 1989). The specimen (MNCN N°128) has been re-studied, and turned out to be an adult *Hipposideros* male, but noticeably smaller (FA 84; GSL 30.1; CBL 26.3; DCC 7.0; ZW 16.2) than specimens of our *H. commersoni* series. The body fur (in alcohol) is yellowish orange and lacks the *H. commersoni*'s typical dark spots on the shoulders. The MNCN N°128's skull, is clearly weaker than a typical *H. commersoni*'s, without any crest and showing duller edges of the rostrum. We now conclude that the specimen MNCN N°128 does not belong to *H. commersoni*; rather, it is a mislabelled *Hipposideros,* probably belonging to the Asian '*diadema*' group of Hill (1963).

Therefore, our series represents the first real *H. commersoni* specimens from Bioko. Their measurements fit will into the range of *H. commersoni gigas* (Rosevear 1965). They were netted across rivers in both cocoa plantations and rain forest and no shelters were found.

Hipposideros cyclops (Temminck, 1853)

Material [18]: Bioko (unknown locality): 1 adult ♀. Malabo-Riaba road, km 2: 6 adult ♀♀. Ericorico river, Malabo-Riaba road, km 3: 1 adult ♀. Vda. Mera plantation, Malabo-Luba road, km 5: 1 adult ♂ and 4 adult ♀♀. Luba: 2 adult ♂♂ and 1 adult ♀. Eolá river, Patio Vivancos, Baney: 1 adult ♀. Borabuopé river, Mallo plantation, Malabo: 1 adult ♂.
Selected measurements: Males: FA [5] mean 67.2 (66.0–68.3); GSL [2] mean 29.3; CCL [2] mean 25.9 (25.7–26.0); DCC [2] mean 8.2 (8.1–8.3); MW [2] mean 12.2 (12.1–12.4); ZW

[2] mean 16.2 (16.1–16.3). Females: FA [13] mean 70.1 (69.0–72.5); GSL [9] mean 29.4 (28.4–30.5); CCL [9] mean 26.0 (25.1–27.0); DCC [9] mean 8.1 (7.7–8.7); MW [9] mean 12.6 (12.3–12.9); ZW [9] mean 16.5 (16.0–17.0).
Remarks: Eisentraut (1964, 1973) included this species in the bat fauna of Bioko based on a photograph by Basilio (1962), but without having seen any specimens. Our series confirms the presence of *Hipposideros cyclops* on Bioko as a quite common bat, and as a typical dweller of trunk holes in both forest and cocoa plantations throughout the island.

Vespertilionidae

Glauconycteris poensis (Gray, 1842)

Material [20]: Ericorico river, Malabo-Riaba road, km 3: 1 ♂ and 1 ♀. Vda. Mera plantation, Malabo-Luba road, km 5: 1 ♀. Bosao river, Malabo-Luba road, km 20: 1 ♀. Apú river, Malabo-Luba road, km 21: 2 ♀♀. Oprocage farm, Moka, Luba: 2 ♂♂ and 1 ♀. Matadero river, Malabo: 1 ♀. Borabuopé river, Mallo plantation, Malabo: 1 ♂ and 7 ♀♀. Ela Nguema, Malabo: 1 ♀. Basilé peak road, km 1: 1 ♂.
Selected measurements: Males: FA [5] mean 38.5 (37.5–39.6); GSL [1] 13.0; CCL [1] 12.9; ZW [1] 9.7; MW [1] 8.5; DCC [1] 4.8. Females: FA [15] mean 39.3, (36.2–41.3); GSL [8] mean 13.0 (12.7–13.5); CCL [8] mean 12.8 (12.5–13.2); ZW [6] mean 9.5 (9.3–9.9); MW [8] mean 8.3 (7.8–8.5); DCC [8] mean 4.7 (4.5–4.9).
Remarks: The species was named *G. poensis* because Bioko island (formerly Fernando Poo) was thought, by mistake, to be the type locality instead of Abo, lower Niger (Aellen 1952). Eisentraut (1964) mentioned only a young *Glauconycteris* tentatively identified as a *G. poensis,* but questioned its presence on Bioko. All the captured specimens show a tawny yellowish fur with tricoloured hairs, typical white flank-stripes and shoulder-spots. The FA measurements fit well within the range of the *G. poensis* given by Rosevear (1965), the skulls from Bioko being a little bigger. Therefore, *Glauconycteris poensis* is confirmed on Bioko island, where it has been netted up to 1300 m a.s.l. (Moka) and where it is apparently common, including within cocoa plantations.

Glauconycteris beatrix Thomas, 1901

Material [4]: Basupú, km 14 Malabo-Luba road: 1 ♀. Matadero river, Malabo: 1 adult ♀. Borabuopé river, Mallo plantation , Malabo: 2 adult ♀♀.
Selected measurement: FA mean 38.6 (36.4–40.2).
Remarks: This is the first record of *Glauconycteris beatrix* from Bioko island, known already from Cameroon (Aellen 1952). The specimens differ from the former species in that they have differently shaped ears and tragus. The fur colour is also notably darker and the white flank-stripes are absent, although one specimen shows small white shoulder-spots (EBD 20503). *Glauconycteris beatrix* has been netted in the same habitats as *G. poensis* in both cocoa plantations and forests, but it is much rarer.

Pipistrellus (Pipistrellus) kuhlii (Natterer, 1817)

Material [4]: Lake Biao, Moka: 3 adult ♂♂ and 1 adult ♀.
Selected measurements: FA [4] mean 35.5 (34.4–37); GSL [4] mean 13.4 (13.0–13.8); CCL [3] mean 12.4 (12.1–12.8); MW [4] mean 7.3 (7.2–7.4); DCC [4] 4.3 (4.1–4.6).
Remarks: All four specimens show the distinctive conic shape of the upper inner incisors and the upper premolar, clearly noticeable from the outside. No white along the wing membrane border, or along the uropatagium is noted, and the measurements match those given for Cameroon specimens (Hill 1968).

This newly recorded species from Bioko island is apparently montane since it has been collected only above 1300 m. *Pipistrellus kuhlii* shows a continuous distribution along a coastal fringe from northern Africa southward through the eastern coast and reaching as far as Cape Province (Hill 1968) *P. kuhlii* is scattered throughout West-Africa. It has been recorded from the Canary Islands (Trujillo 1991); La'youn (El Aaiún), Western Sahara (Ibáñez and Fernández 1989); the Cape Verde Islands (Azzaroli Puccetti and Zava 1988); and from some mountain areas of western tropical Africa, such as Mount Nimba (Hill 1982) and Mount Cameroon (Hill 1968).

Pipistrellus (Neoromicia) tenuipinnis (Peters, 1872)

Material [4]: Bosao river, Malabo–Luba road, km 18: 1 adult ♀. Borabuopé river, Mallo plantation, Malabo: 3 adult ♀♀.
Selected measurements: FA [4] mean 31.6 (31.0–32.0); MW [1] 7.0; ZW [1] 8.0; DCC [1] 4.4.
Remarks: *P. tenuipinnis* is widespread in western and central Africa (Rosevear 1965) and it is well known on nearby Mount Cameroon (Aellen 1952). The specimens collected show typically whitish and translucent wings. They represent the first record of *P. tenuipinnis* from Bioko, where they have been netted mainly in cocoa plantations.

Pipistrellus (Neoromicia) cf. *capensis* (Smith, 1829)

Material [18]: Ericorico river, Malabo–Riaba road, km 3: 1 adult ♂, 1 adult ♀. Grande river, Riaba: 1 adult ♀. Vda. Mera plantation, Malabo–Luba road, km 3: 2 adult ♀♀. Sampaca, Malabo–Luba road, km 7: 2 adult ♀♀. Bosao river, Malabo–Luba road, km 20: 1 adult ♀. Musola river, Luba: 2 adult ♀♀. Eolá river, Patio Vivancos, Baney: 1 adult ♀. Borabuopé river, Mallo plantation, Malabo: 1 adult ♂ and 5 adult ♀♀. Basilé village, Malabo: 1 adult ♂.
Selected measurements: Males [3]: FA mean 34.8 (34.5–35.0); GSL mean 13.9 (13.8–14.0); CBL mean 12.9 (12.8–13.0); DCC mean 4.3 (4.2–4.4). Females: FA [15] mean 35.4 (34.0–37.0); GSL [13] mean 13.9 (13.6–14.4); CBL [13] mean 13.1 (12.7–13.6); DCC [13] mean 4.4 (4.2–4.6); ZW [6] mean 9.0 (8.8–9.3).
Remarks: All Bioko specimens have dull brown fur. Their average measurements are slightly larger than the values given by Koopman (1975) for *P. capensis*, but agree with those given by Rosevear (1965). The systematics of this group remain very entangled, especially regarding the West African forms. We therefore consider our specimens at present as *Pipistrellus (N.)* cf. *capensis*, which is the first record of the species from Bioko island.

Molossidae

Mops (Xiphonycteris) spurrelli (Dollman, 1911)

Material [32]: Ericorico river, Malabo–Riaba road, km 3: 3 adult ♂♂ and 17 adult ♀♀. Grande river, Riaba: 2 adult ♂♂. Timbabé river, Malabo–Luba road, km 3: 1 adult ♀. Apú river, Malabo–Luba road, km 21: 1 adult ♂ and 7 adult ♀♀.
Selected measurements: Males: FA [6] mean 28.7 (28.0–29.7); GSL [2] mean 15.9 (15.9–16.0); CBL [2] mean 14.7 (14.7–14.8); CCL [2] 14.5; DCC [2] mean 4.6 (4.5–4.8); ZW [2] mean 10.2 (10.0–10.5) MW [2] mean 9.5 (9.4–9.6). Females: FA [26] mean 28.2 (27.0–29.6); GSL [12] mean 15.4 (15.1–15.8); CBL [12] mean 13.9 (13.6–14.3); CCL [12] 13.7 (13.3–14.1); DCC [12] mean 3.9 (3.5–4.1); ZW [12] mean 9.6 (9.3–10.0); MW [12] mean 9.3 (9.1–9.3).
Remarks: This species had been known from Bioko by one specimen from Banapá

(Basilio 1962) and another specimen without specific locality (Kock 1969). Its presence on the island was, therefore, questioned (Hayman and Hill 1971; Eisentraut 1973). A new series confirms the presence of *Mops spurrelli* on the island; surprisingly, it seems to be the most common molossid. It was captured along most of the rivers suitable for the species on the island.

Mops (Xiphonycteris) thersites (Thomas, 1903)

Material [24]: Grande river, Riaba: 2 adult ♂♂, 9 adult ♀♀ and 1 subadult ♀. Ericorico river, Malabo–Riaba road, km 3: 4 adult ♀♀. Apú river, Malabo–Luba road, km 21: 1 adult ♀. Lopesi river, Malabo: 2 adult ♂♂ and 4 adult ♀♀. Matadero river, Malabo: 1 adult ♀.

Selected measurements: Males [4]: FA mean 38.7 (38.0–39.5); GSL mean 20.3 (18.9–21.3); CBL mean 18.1 (17.6–18.5); CCL mean 17.4 (16.9–17.7); DCC mean 5.6 (5.4–6.0); MW mean 11.3 (10.9–11.8); ZW mean 12.5 (11.9–12.8). Females: FA [19] mean 38.6 (37.0–40.2); GSL [18] mean 19.1 (18.5–20.0); CBL [18] mean 17.4 (16.7–17.9); CCL [18] mean 16.8 (16.3–17.2); DCC [18] mean 5.2 (4.9–5.4); MW [18] mean 11.0 (10.6–11.3); ZW [18] mean 11.9 (11.7–12.2).

Remarks: There has been some confusion about the middle-sized molossids of Bioko island. A single specimen from Bantabaré was first identified as *Chaerephon pumila* (Dobson 1878) and subsequently as *Mops leonis* (Thomas 1908), at present *M. brachypterus*. Consequently, both species were long accepted as inhabitants of the island, (e.g. Hayman and Hill 1971). Eisentraut (1964) mentioned both species from the island but later considered that the specimen may actually represent *Mops thersites* (Eisentraut 1973), although the record is still accepted as *Chaerephon pumila* elsewhere (Koopman 1993).

The new series confirms the presence of *Mops thersites* on the island as a common bat, at least in the lowland zones and cities.

Discussion

Among Bioko's previously known bat species, *Eptesicus platyops, Chaerephon pumila, Mops brachypterus* and *Nycteris hispida* have not been captured in spite of our intense netting efforts. The absence of *C. pumila* and *M. brachypterus* seems to confirm Eisentraut's (1973) statement of a systematic mistake. We agree that these last two species should not be included in the checklist of Bioko. Finally, only three *Nycteris hispida* specimens are known from Bioko, all of them from the 19th century. We have checked the identity of one of them (MNCN N° 76) and it apparently belongs to *N. hispida*, although its tragus is not semilunate and only one incisor can be considered trifid because of wear. The remaining two specimens have recently been studied by Van Cakenberghe and De Vree (1993).

The newly found bat species, and the confirmed ones, strengthen the resemblance of Bioko's bat fauna to that of the Mount Cameroon zone. Almost all of these bats have previously been recorded there. Finally, the absence of endemism in the bat fauna of Bioko is apparently confirmed. This is in contrast to other mammal groups like such as primates, which reach up to 70 % of endemism at a subspecific level (Butynski and Koster 1986). Bioko, a typical landbridge island, was connected with the mainland relatively recently, about 6,000 years ago (Thys van den Andenauerde 1967). This fact, coupled with the high vagility of bats, is likely to have hampered any speciation process among the group on Bioko.

Acknowledgements

We wish to thank Antonio Ayong Nguema for his help, support, and friendship throughout so many years of field work, and Mr. Leandro Mbomío Nsué, former Minister of Culture of Equatorial Guinea, for his encouragement of and confidence in our work. Agie Reeves, Andy, Caroline Green and Claudia Keller for their kind help with the English and German translations. The work was supported by the Oficina de Cooperación con Guinea Ecuatorial [at present, Instituto de Cooperación para el Desarrollo] of the Spanish Ministerio de Asuntos Exteriores with the cooperation of the Asociación de Amigos de Doñana.

Zusammenfassung

Beitrag zur Kenntnis der Chiropterenfauna der Insel Bioko, Äquatorial-Guinea

Die Fauna der Insel Bioko (ehemals Fernando Poo, Äquatorial-Guinea) ist schon Objekt verschiedener Studien gewesen, aber dennoch nicht vollständig bekannt, besonders was die Chiropterenfauna angeht. Die Fledermausarten *Hipposideros commersoni, Glauconycteris beatrix, Pipistrellus kuhlii, P. tenuipinnis* und *P.* cf. *capensis* werden zum erstenmal für die Insel erwähnt. Das Vorkommen der Arten *Myonycteris torquata, Taphozous mauritianus, Nycteris arge, Hipposideros cyclops, Glauconycteris poensis, Mops spurrelli* und *M. thersites*, in früheren Veröffentlichungen als zweifelhaft erwähnt, wird nun auf Bioko bestätigt. Mit diesen Resultaten wird die Liste der Fledermausarten für die Insel Bioko um 25 % erweitert und zählt hiermit 26 Arten.

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Authors' address: Dr. JAVIER JUSTE B. and Dr. CARLOS IBÁÑEZ, Estación Biológica de Doñana, C.S.I.C., Aptdo. 1056, E-41080 Sevilla, Spain

Z. Säugetierkunde 59 (1994) 282–288

ISSN 0044-3468

Distribution of the Cabrera water shrew (*Neomys anomalus*) in Northeastern Spain

By I. Torre and J. L. Tella

Departamento de Biología Animal (Vertebrados), Facultad de Biología, Universidad de Barcelona, Barcelona, Spain

Receipt of Ms. 20. 4. 1993
Acceptance of Ms. 5. 2. 1994

Abstract

This study deals with the range of the Cabrera water shrew (*Neomys anomalus*) in the northeast Iberian peninsula and the ecological factors that may determine its distribution. Information is provided on 26 new sites, including the first records of the species on the southern slope of the Pyrenees. In these mountains, where the water shrew (*Neomys fodiens*) lives, the Cabrera water shrew (*N. anomalus*) was found at high altitudes and also below the range occupied by the former species. In the remainder of the study area its distribution seems to be conditioned by the hydrographic network characteristics, showing mediterranean preferences.

Introduction

The geographical distribution of the Cabrera water shrew in the Iberian peninsula has not been thoroughly studied. Although a number of references suggest a widespread range (Faus 1991), in the NE Iberian peninsula this species has been found only occasionally, perhaps due to its scarcity or low detectability through sampling methods (López-Fuster et al. 1992). Its distribution and ecological requirements have been supposed on the basis of a small number of locations (Gosálbez 1987; Jiménez et al. 1989; Faus 1991), or generalization from extensive data of this species over the entire range of its European distribution (Spitzenberger 1990). The aim of this study was to describe these aspects in greater detail, by analysing both information on new and previously known locations.

Material and methods

The study was carried out in the autonomous regions of Aragón, Catalonia and in the province of Castellón. The altitude of the regions studied ranged from sea level to 3404 m above sea level. There are six bioclimatic zones belonging to the Eurosiberian and Mediterranean regions (Rivas-Martínez 1983). Therefore, almost all the climatic and ecological characteristics of the Iberian peninsula can be found in the study area. Figure 1 shows the principal geographic characteristics of the study area.

A review of the literature revealed 46 reports of the Cabrera water shrew from 24 locations (Miller 1912; Nadal and Palaus 1967; Garzón et al. 1971; Sans-Coma 1973; Vericad and Meylan 1973; González 1975; Pelayo 1979; Gosálbez et al. 1985; Rubio 1985; Arrizabalaga et al. 1986; Gosálbez 1987; Jiménez et al. 1989; Spitzenberger 1990; Faus 1991; López-Fuster et al. 1992; Torre et al. 1992).

Our prospections were centred on wide areas where the presence of this species was unknown. The analysis of barn owl (*Tyto alba*) pellets collected from 1985 to 1992 provided 15,486 small-mammal preys from 33 different sites in the Ebro depression. Specimens were also captured at three different sites: Alt Aneu (Pyrenees), by placing 100 mouse traps for four days (December 1987) along the Noguera Pallaresa river and in alpine meadows; Híjar (Ebro depression), with the same number of mouse traps for three days (February 1988) along the Martin riverside and some irrigation channels; Ateca (on the Iberian range spurs), using 75 "pitfall" mouse traps at the Manubles riverside for 6 days (March 1990). We also obtained information about the species from two nature magazines and by interviewing some specialists working on small mammals in the study area.

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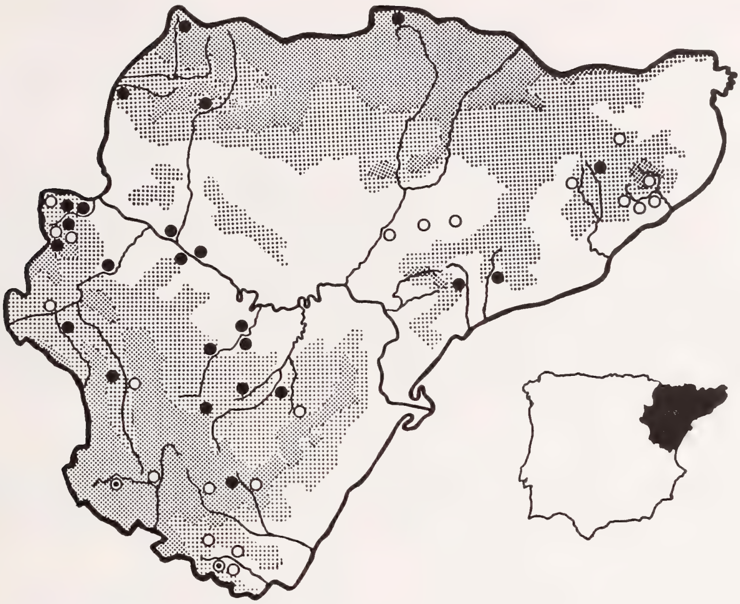

Fig. 1. Orography, hydrographic basins, location of the study area and sites where *Neomys anomalus* were recorded (Black circles = new localities; white circles = localities cited in literature; lightly dotted area = > 500 m.a.s.l.; densely dotted area = > 1000 m.a.s.l.)

Those Cabrera water shrews trapped or found dead were identified by morphological characteristics (Cabrera 1914; Spitzenberger 1990). The skulls found in the pellets were identified using the discriminant formula given by Bühler (1964). The skulls obtained by collaborators have also been determined by us. Reports of observations of live water shrews were only considered if the informant was an experienced person.

From each location we recorded the altitude above sea level, river flow, rainfall and annual average temperature (Forteza 1985; León et al. 1987; M.O.P.U. 1988; Bosque and Vila 1992). We have only treated the number of localities because there is a narrow relation between number of localities and number of *Neomys anomalus* for every variable considered: altitude ($r = 0.94$, $p < 0.001$), temperature ($r = 0.97$, $p < 0.001$), rainfall ($r = 0.95$, $p < 0.0001$), and water flow ($r = 0.95$, $p < 0.002$). Since every sampling method itself provides little information about the species (López-Fuster et al. 1992) we treated all localities together. The results obtained may correspond to a biased sample, but could be considered as an approximation of the real ranges occupied by this species.

Results and discussion

The presence of *Neomys anomalus* was recorded at 26 new sites and two previous ones. We found 45 animals, added to those already described in the literature, totals 91 Cabrera water shrews, belonging to 50 different sites in the NE of the Iberian peninsula. Figure 1 shows the situation of records of *Neomys anomalus* in the study area, and the table provides details on records sites, altitude, associated rivers, and number as well as origin of *Neomys anomalus*.

With regard to the altitude (Fig. 2A), the species was irregularly distributed between 180 and 1,850 m.a.s.l., but most of the records were made below 1,000 m (96 %), in contrast with its preference for highlands in central Europe (Fons et al. 1980; van Laar 1983; Taberlet 1984). The species was also found at variable river flows (Fig. 2B), from rivers with less than 2 m^3/s to the Ebro river (261 m^3/s), suggesting that its presence was

Sampling sites, altitude, associated river, number and origin of *Neomys anomalus*

Locality	U.T.M.	Altitude	Hidrographic basin	Nº *Neomys*	Source	Authors
Zorita del Maest. (CS)	30TYL3912	662	Bergantes	2	PE	Faus (1991)
Villahermosa Río (CS)	30TYK1855	780	Villahermosa	1	OB	Jiménez et al. (1989)
Jérica (CS)	30TYK0919	420	Palancia	1	FD	Jiménez et al. (1989)
Teresa (CS)	30TYK0019	636	Palancia	1	OB	Jiménez et al. (1989)
Teresa (CS)	30TYK0019	636	Palancia	1	PE	Jiménez et al. (1989)
Bejís (CS)	30TXK9620	800	Palancia	1	OB	Jiménez et al. (1989)
Bejís (CS)	30TXK9620	800	Palancia	2	OB	J. Verdejo (pers. com.)
Barracas (CS)	30TXK9632	981	—	2	TR	Miller (1912)
Mora de Rubielos (TE)	30TXK9158	1030	Mora (Mijares)	1	TR	Garzón et al. (1971)
Mora de Rubielos (TE)	30TXK9158	1030	Mora (Mijares)	1	PE	González (1975)
Albarracin (TE)	30TXK3174	1100	Guadalaviar	2	TR	Vericad and Meylan (1973)
Albarracin (TE)	30TXK3174	1140	Guadalaviar	1	OB	J. Verdejo (pers. com.)
Teruel (TE)	30TXK5968	870	Guadalaviar	1	OB	Jiménez et al. (1989)
Linares de Mora (TE)	30TYK0765	1220	Linares	1	OB	J. Verdejo (pers. com.)
Linares de Mora (TE)	30TYK0764	1180	Linares	1	OB	J. Verdejo (pers. com.)
Híjar (TE)	30TYL1663	230	Martin	4	PE	(this study)
Albalate del A. (TE)	30TYL0751	400	Martin	1	TR	J. I. Pino (pers. com.)
Albalate del A. (TE)	30TYL0448	400	Martin	1	PE	Gosálbez et al. (unpubl.)
Mas de las Matas (TE)	30TYL3224	494	Guadalope	1	PE	Gosálbez et al. (unpubl.)
Berge (TE)	30TYL1626	719	Guadalopillo	3	PE	Gosálbez et al. (unpubl.)
Cañizar del O. (TE)	30TXL9919	950	Estercuel	1	FD	L. Bolea (pers. com.)
Sos del Rey C. (Z)	30TXN4606	654	Onsella	1	PE	J. M. Sánchez (pers. com.)
Ateca (Z)	30TXL0176	608	Jalón	7	PE	Torre et al. (1992)
Ricla (Z)	30TXL0707	377	Jalón	1	PE	J. M. Sánchez (pers. com.)
Gallocanta (Z)	30TXL3042	1000	—	9	PE	Burguete and Guiral (unpubl.)
Gallocanta (Z)	30TXL3042	1000	—	1	PE	V. Pedrocchi (pers. com.)
Calamocha (Z)	30TXL4333	880	Jiloca	1	OB	Jiménez et al. (1989)
Monasterio Piedra (Z)	30TXL0261	800	Piedra	1	OB	J. M. Sánchez (pers. com.)
Monasterio Piedra (Z)	30TXL0261	800	Piedra	1	OB	J. Guiral (pers. com.)
La Alfranca (Z)	30TXM8608	180	Ebro	1	OB	F. Hernández (pers. com.)
La Alfranca (Z)	30TXM8608	180	Ebro	1	PE	F. Hernández (pers. com.)
La Cartuja (Z)	30TXM8108	180	Ebro	1	OB	F. Hernández (pers. com.)
Juslibol (Z)	30TXM3042	180	Ebro	1	PE	F. Hernández (pers. com.)
Tarazona (Z)	30TXM0540	480	Queiles	1	TR	López-Fuster et al. (1992)
Agón (Z)	30TXM2736	310	Huecha	1	FD	E. Pelayo (pers. com.)

Borja (Z)	30TXM2131	455	Huecha	1	OB	E. Pelayo (pers. com.)
Talamantes (Z)	30TXM0919	1000	Valdetreviño	1	OB	Pelayo (1979)
Talamantes (Z)	30TXM0920	880	Valdetreviño	1	OB	Pelayo (1979)
Añón (Z)	30TXM0225	1300	Morca (Huecha)	1	OB	J. M. Sánchez (pers. com.)
Añón (Z)	30TXM0626	836	Huecha	1	TR	López-Fuster et al. (1992)
Alcalá de Moncayo (Z)	30TXM0827	766	Huecha	2	PE	Arrizabalaga and Montagud (unpubl).
Pard. Bataragüá (H)	30TXN9600	650	—	1	PE	J. Guiral (pers. com.)
Ansó (H)	30TXM8350	1660	Alpine meadows	1	FD	J. L. Rivas (pers. com.)
Leida (L)	32TCG0210	223	Segre	9	TR	Miller (1912)
Mollerussa (L)	31TCG2410	246	Urgell channel (Segre)	2	PE	Nadal and Palaus (1967)
E. de Montcortés (L)	31TCG1952	450	—	?	?	Spitzenberger (1990)
Alt Aneu (L)	31TCH4336	1850	Alpine meadows	1	FD	(this study)
La Riba-Vilavert (T)	31TCF4575	390	Francolí	1	OB	R. R. Jarillo (pers. com.)
Sta Perpetua de G. (T)	31TCF9066	500	Gaià	1	TR	J. A. Regy (pers. com.)
S. M. Palautordera (B)	31TDG5214	260	Tordera	3	PE	Arrizabalaga et al. (1986)
Campins (B)	31TDG5418	260	Tordera	1	PE	Arrizabalaga et al. (1986)
Cànoves (B)	31TDG4616	344	Torrent Valfornis	1	OB	Rubio (1985)
Castellterçol (B)	31TDG2622	726	Tenes (Besós)	1	PE	Sans-Coma (1973)
Ayguafreda (B)	31TDG3724	406	Martinet (Congost)	1	TR	R. Margalef jr. (pers. com.)
S. Bartomeu del G. (B)	31TDG6321	900	—	1	PE	Gosálbez et al. (1985)
Arbúcies (G)	31TDG5929	295	Riera de Arbúcies	2	PE	Sans-Coma (1973)

Provinces: CS = Castellón; TE = Teruel; Z = Zaragoza; H = Huesca; L = Lleida; T = Tarragona; B = Barcelona; G = Girona. Source: PE = barn owl pellets; OB: observation; TR = trapped; FD = found dead.

not conditioned by water flow. As has been stated before (Amores 1975; Gosálbez 1987; Spitzenberger 1990), the Cabrera water shrew lives distant from the streams, its distribution perhaps being favoured by the presence of irrigation channels (Cortes and Gil 1984). The Cabrera water shrew evidently has a wide climatic range (Fig. 2C, D), showing clear mediterranean trends: annual average temperatures were between 10 and 16 °C for 90 % of the sites, and rainfall was lower than 800 mm in 92 % of the sites. The rainfall index does not constrain its distribution; these results are in contrast to those observed by Triano (1985) in SW Spain. Our results agree with those found by González and Román (1988) in the province of Burgos.

Concerning its geographical distribution, Cabrera (1914) pointed out its presence in the Spanish Pyrennes, but the lack of evidence available for this statement shed some doubts on its authenticity. Later researchers (e.g. Vericad 1970; Sans-Coma and Margalef 1981; Gil et al. 1986; Moreno and Barbosa 1992) did not find this species in these mountains, and a recent review (Spitzenberger 1990) did not consider the presence of the Cabrera water shrew in the Spanish Pyrenees. We provide the first confirmed records for their presence here. These may suggest a low density distribution along the axial Pyrenees, where the species may occupy alpine meadows far from streams over 1,600–1,800 m.a.s.l., and streams of the Prepyrenean foothills below 1,000 m.a.s.l. This distribution could be conditioned by the presence of the water shrew (*Neomys fodiens*), which lives in this area over 900–1,000 m.a.s.l. (Gosálbez 1987), as a result of the altitudinal and habitat

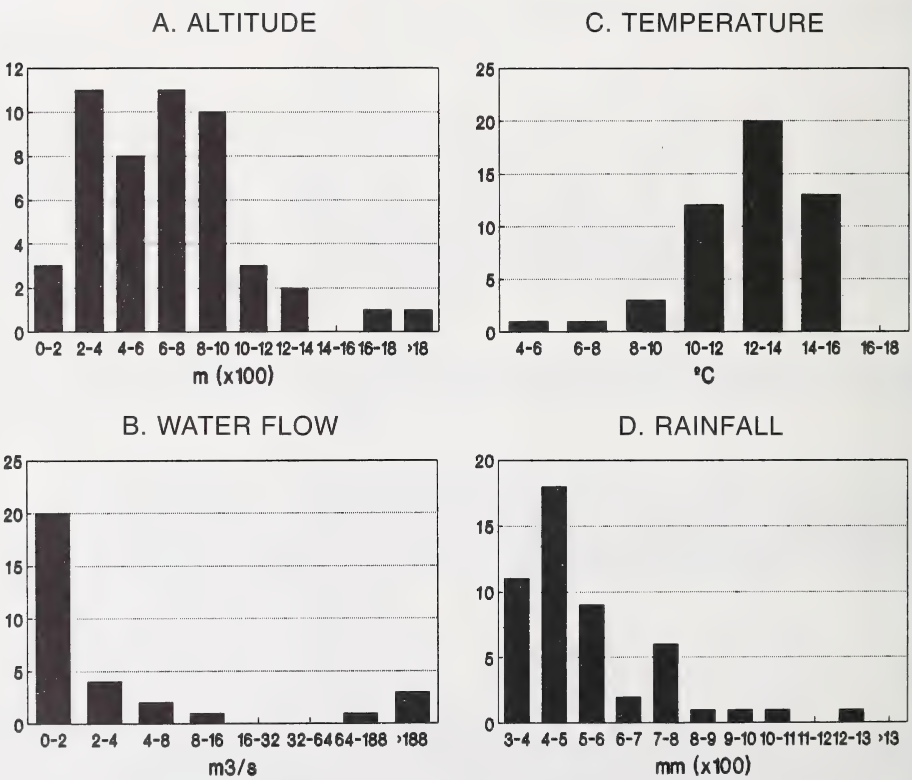

Fig. 2. Frequency of distribution of the localities where *Neomys anomalus* was found according to altitude (A), river water flow of the nearest station to the site of sampling (B), annual average temperature (C), and rainfall (D)

segregation sometimes reported between both species (SPITZENBERGER 1990). Otherwise, the information recorded is insufficient to confirm this hypothesis, more detailed studies being required about the species in the Pyrenees. In the remainder of the study area, where *N. fodiens* is absent, *N. anomalus* is widely distributed along the Iberian range, most probably reaching the arid regions of the Ebro depression through the river systems. The presence of the Cabrera water shrew in two separated centres of the Catalan range confirms its distribution along these mountains, discussed by JIMÉNEZ et al. (1989) and FAUS (1991), but we were unable to determine whether a continuity exists from the Iberian range to the Pyrenees through the Catalan range.

Acknowledgements

We are very grateful to A. ARRIZABALAGA, J. VERDEJO, E. PELAYO, F. HERNÁNDEZ, J. M. SÁNCHEZ, L. BOLEA, J. GUIRAL, R. MARGALEF Jr., J. MARTÍN, E. MONTAGUD, V. PEDROCCHI, A. PÉREZ, J. I. PINO, J. A. REGY, J. L. RIVAS and R. R. JARILLO for allowing us to use their unpublished data.

Drs. J. GOSÁLBEZ, M. J. LÓPEZ-FUSTER, J. VENTURA, E. CASTIÉN, J. NADAL, and an anonymous reviewer provided comments on an earlier draft. We also thank T. BALLESTEROS, T. BORAU, S. CARBÓ, A. FARNÓS, F. V. FAUS, M. A. GARCÍA, F. GONZÁLEZ, I. GRABULOSA, V. FERNÁNDEZ, J. JIMÉNEZ, E. MORENO, R. MILARA, A. REQUEJO, J. RUIZ-OLMO and J. SOLÉ for their help. C. GORTÁZAR translated the abstract into German, and M. VILLARROEL improved the English text.

Zusammenfassung

Verbreitung der Sumpfspitzmaus (Neomys anomalus) im Nordosten Spaniens

Beschrieben werden die Verbreitung der Sumpfspitzmaus im Nordosten Spaniens sowie die ökologischen Faktoren, die ihr Verbreitungsgebiet bestimmen. Wir informieren über 26 neue Fundorte.

Auf der Südseite der Pyrenäen, wo die Sumpfspitzmaus zum ersten Male gefunden wurde, lebt die Art auf alpinem Grasland, wahrscheinlich aufgrund einer Kompetenzbeziehung zu *N. fodiens*. Im restlichen Studiengebiet, wo *Neomys fodiens* nicht auftritt, findet man die Sumpfspitzmaus in verschiedenen Klima- und Höhenlagen, obwohl mediterrane Umgebungen bevorzugt werden. Die Sumpfspitzmaus findet man in den axialen Pyrenäen, im Ebrotalkessel und der Umgebung der iberischen Gebirgskette. Noch ist nicht klar, ob *N. anomalus* vom Küstengebirge bis in die östlichen französischen Pyrenäen eine zusammenhängende Verbreitung aufweist. Die Anwesenheit der Sumpfspitzmaus wird andererseits von dem hydrographischen Netz bestimmt. Die Spitzmaus breitet sich über Ströme und Bewässerungskanäle aus und erreicht mitunter Trockenbiotope, die aber immer feuchte Mikrohabitate aufweisen.

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Authors' addresses: Ignacio Torre, Departamento de Biología Animal (Vertebrados), Facultad de Biología, Universidad de Barcelona, Avda. Diagonal 645, E-08028 Barcelona and José L. Tella, Estación Biológica de Doñana (CSIC), Avda. Ma Luisa s/n, Pabellón del Perú, E-41013 Sevilla, Spain

Z. Säugetierkunde 59 (1994) 289–298

ISSN 0044-3468

A report on the distribution of small mammals from Namibia

By J. O. Matson and B. R. Blood

Department of Biological Sciences, San Jose State University, San Jose; Department of Physical Therapy, Mt. St. Mary's College, Los Angeles; and Research Assoc., Sect. Mammals, Natural History Museum, Los Angeles, California, USA

Receipt of Ms. 4. 2. 1994
Acceptance of Ms. 28. 4. 1994

Abstract

A sample of small mammal species from 37 pooled localities throughout Namibia was used to assess ecological and zoogeographical distribution patterns. Multivariate techniques (Cluster Analysis and Principal Components Analysis) revealed an essentially ecological distribution based upon climate/vegetation types within Namibia. Five major ecological areas are defined which correspond to previously described vegetation and zoogeographic regions.

Introduction

Searching for and recognizing patterns in nature is one of the fundamental endeavors of scientists. Spatial patterns of species distributions belong to the realms of ecology and biogeography. While the ultimate causes of species distributions are evolutionary and require historical explanations, identifying the patterns are an essential first step in the process.

Mammalian taxonomy and distribution in southern Africa are poorly understood (Dippenaar et al. 1983; Skinner and Smithers 1990). Analyses in southern Africa (Rautenbach 1978) and especially of Namibia (Coetzee 1983) have greatly increased our understanding of mammalian distribution patterns in this part of the African continent. Namibia represents a major portion of the Southwest Arid Biogeographic Zone. The fauna of this zone is considered to be quite distinct and to have had a long evolutionary history (Bigalke 1972).

The Natural History Museum of Los Angeles County (LACM) has an extensive collection (over 6,500 specimens) of mammals from Namibia. While these specimens have never been reported upon in the literature, Coetzee's (1983) did use the field identifications of some of these as a basis for his analysis of distribution patterns of mammals in Namibia. In our curation of this collection we noted that there were numerous misidentifications and errors. We have corrected these and use the revised material as the basis for the following analyses.

The major question we ask is "What geographic and/or ecological patterns can be discerned from the specimens from Namibia housed in the LACM?" Three Biotic Zones are recognized in Namibia by Skinner and Smithers (1990), Namib Desert, Southwest Arid, and Southern Savanna Woodland. These are the same as defined by Rautenbach (1978). Coetzee (1983) also recognized and defined these zones as mammalian Zoogeographical Provinces within Namibia. Since Coetzee (1983) had presented an analysis of mammalian distribution patterns in Namibia, we wanted to use the current material as a comparable sample. If the faunal areas recognized by Coetzee (1983) have biological validity, then an analysis of a subsample of mammals from Namibia should also reflect similar patterns. In addition we use the results of this analysis to suggest testable hypotheses concerning mammalian distribution patterns.

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Material and methods

Because the LACM collection concentrated upon small mammals, we restricted our analysis to the following orders, Insectivora Macroscelidea, Lagomorpha, Rodentia, and Hyracoidea. Mammalian taxonomy used herein follows that of SKINNER and SMITHERS (1990) and MEESTER et al. (1986). However, these authors recognize but a single species of hyrax from Namibia, *Procavia capensis*. Because there are definite morphological differences in the specimens we have on hand we prefer to recognize two species for our analyses, *P. capensis* and *P. welwitschii*.

Localities were used as operational taxonomic units (OTU's sensu SOKAL and SNEATH 1963). Since several localities were represented by only a few species, we pooled nearby localities. Figure 1 is a map of the pooled localities. A list of the localities and species is given in tables 1 and 2. The pooled localities were used as the OTU's for the analyses.

Fig. 1. Map of Namibia showing the pooled localities used in the analysis of mammalian distributions

Cluster analysis

Similarity between OTU's was calculated separately using the squared Euclidian distances and the "Faunal Resemblance Factor" (FRF) utilized by COETZEE (1983). The OTU's were clustered using the unweighted pair group method with arithmetic averages as suggested by SNEATH and SOKAL (1973). While both similarity matrices produced relatively equivalent groupings, the results presented here are based upon the squared Euclidean distances.

Principle components analysis (PCA)

OTU's were subjected to PCA, based upon a correlation matrix, to select an optimal subset of species (variables) from our sample that would bring about an ordination of the pooled localities. In order to simplify interpretation of the analysis, low PC scores are those OTU's which have a cummulative loading of less than −0.99 while high PC scores are those greater than +1.00.

All computations were done using an IBM/PC 386 using the SPSS statistical packages (NORUSIS 1988).

Table 1. **Collecting localities in Namibia**

Number in parentheses at end of locality indicates the pooled locality of Fig. 1

1. Kaokaland Area I; Opuwa, 106 km N, 65 km W Epupa Valley (1).
2. Kaokaland Area I; Opuwa, 66 km N, 84 km W Etengua (1).
3. Kaokaland Arae I; 63 km N, 55 km W, near Otjiangasemo (1).
4. Kavango Area I; Nkurrenhura, South Africa Police Camp (3).
5. Kaokaland Area I; 39 km N 130 km W Marienfluss (2).
6. Kavango Area I; 25 km N, 113 km W Rundu, Kanana (3).
7. Kaokaland Area I; Otju (2).
8. Kavango Area I; 9 km S, 84 km E Rundu, Shitemo (4).
9. Kaokaland Area I; Orumpebe (2).
10. Kavango Area I; 4 km S, 18 km E Andara, Bagani (5).
11. Kavango Area I; 81 km S, 73 km W Rundu, Tsotsana (6).
12. Kavango Area I; 66 km S, 113 km E Rundu, s fork nr N fork, Omuramba (4).
13. Tsuemb Dist; 45 km N, 33 km E Tsuemb, Wildernis 882 (7).
14. Grootfontein Dist; 80 km N, 93 km E Grootfontein, Tiervlei 1022 (6).
15. Damaraland; 6 km SE Sesfontein 207 (8).
16. Outjo Dist; 37 km N, 28 km W Kamanjab, Ermo 646 (9).
17. Tsumeb Dist; 40 km WNW Grootfontein, Ghaub Farm 47 (7).
18. Grootfontein Dist; 30 km ENE Otavi, Sumas Farm 746 (7).
19. Grootfontein Dist; 35 km E Omkrap 218 (11).
20. Outjo Dist; 41 km N, 45 km E Outjo, Pirre 345 (10).
21. Damaraland; Palmwag 702 (8).
22. Outjo Dist; Westfallen 245 (9).
23. Grootfontein Dist; 8 km S, 4 km W Otavi, Elephantenberg 792 (7).
24. Grootfontein Dist; 25 km S, 36 km E Grootfontein, Okamaruru 220 (11).
25. Damaraland; Krone 721 (8).
26. Hereroland East; 58 km N, 108 km E Otijinunu (12).
27. Otijiwarongo Dist; 52 km ESE Otijiwarongo, Okosongomingo Farm 148 (13).
28. Otijiwarongo Dist; 9 km S, 11 km E Kalkfeld, Elshorst 90 (14).
29. Otijiwarongo Dist; 78 km S, 48 km E Otijiwarongo, Ousema 201 (13).
30. Omaruru Dist; 35 km N, 27 km W Omaruru, Eausiro W 100 (15).
31. Hereroland East; 7 km N, 21 km E Otijinunu (12).
32. Okahanhdja Dist; 75 km N, 117 km E Okahanhdja, Kalidona 277 (16).
33. Omaruru Dist; 8 km N, 9 km W Uitspan 59 (= Kompanenosiid 59) (15).
34. Omaruru Dist; 18 km S, 6 km E Omaruru, Kamombande 86 (15).
35. Gobabis Dist; 117 km N, 39 km E Gobabis, Gelukwater 681 (17).
36. Omaruru Dist; Erongo West 83 (15).
37. Gobabis Dist; 67 km N, 82 km W Gobabis, Kambingana 204 (18).
38. Gobabis Dist; 64 km N, 103 km E Gobabis, Oostenwald 447 (19).
39. Karibib Dist; 17 km S, 7 km W Usakos, Naob 69 (21).
40. Karibib Dist; 47 km S Wilhelmstal, Okandukaseibe Farm 27 (22).
41. Windhoek Dist; 24–30 km N, 68 km E Windhoek, Okatumba South 149 (23).
42. Gobabis Dist; 41 km N, 2 km W Gobabis, Eava 383 (20).
43. Karibib Dist; Nordenberg 76 (21).
44. Karibib Dist; 35 km S, 3 km W Usakos, Dorstrivier 13 (21).
45. Windhoek Dist; 71 km ENE windhoek, Muambo 130 (23).
46. Windhoek Dist; 10 km N, 68 km E Windhoek, Springbock Valley 132 (23).
47. Karibib Dist; 73 km S, 3 km E Bethal Farm (24).
48. Gobabis Dist; 40 km S, 88 km E Gobabis, Uithou 366 (27).
49. Swakopmund Dist; 8 km E Swakopmund, Swakopmund River (28).
50. Windhoek Dist; 81 km SW Wasservallei 382 (25).
51. Windhoek Dist; 110 km E Windhoek, Arnhem Farm 9 (26).
52. Windhoek Dist; Autabib 100 (26).
53. Windhoek Dist; 10 km N, 31 km W Rehoboth, Naos 46 (29).
54. Rehoboth Dist; Wostel 256 (29).
55. Windhoek Dist; 9 km S, 59 km W Rehoboth, Isabis Farm 19 (29).
56. Gobabis Dist; 75 km S, 24 km W Gobabis, Mentz 65 (30).
57. Rehoboth Dist; Nauzerus West 229 (32).
58. Windhoek Dist; Solitare 412 (31).
59. Rehoboth Dist; Billisport 172 (32).
60. Mariental Dist; Mibela 200 (30).

Table 1 (continued)

61.	Maltahoe Dist; 53 km S, 110 km W Maltahoe, Gorrasis 99 (34).
62.	Mariental Dist; Asanib 294 (33).
63.	Mariental Dist; vicinity of Twee River (33).
64.	Luderitz Dist; 77–81 km WNW Helmeringhausen, edge of Kanaan Farm 104 (34).
65.	Bethanie Dist; 23 km WNW Helmeringhausen, Barby Farm 26 (35).
66.	Keetsmanshoop Dist; 89 km ENE Koes, Welverdiend Farm 328 (33).
67.	Bethanie Dist; Odendorf 43 (36).
68.	Keetsmanshoop Dist; Spitzkoppeost 159 (36).
69.	Keetsmanshoop Dist; Gaibis 226 (33).
70.	Keetsmanshoop Dist; Reinfels 125 (36).
71.	Keetsmanshoop Dist; Naute 119 (36).
72.	Keetsmanshoop Dist; Kochena 74 (37).
73.	Keetsmanshoop Dist; Warmfontien 280 (37).

Results and discussion

Cluster analysis

Inspection of the dendrogram (Fig. 2) indicates that there are two major clusters and five minor clusters. Geographically, these are more easily shown in figures 3 and 4. Essentially, the two major clusters (Fig. 3) separate the country into west/southwest and northeast regions. The five minor clusters shown in figure 4 correspond fairly well with the Faunal areas described by Coetzee (1983) and to the vegetation types of Giess (1971). These five clusters are as follows (using terminology from Giess 1971): 1) Namib Desert, Southern Kalahari Desert, and Dwarf Shrub areas; 2) Escarpment and Mopane Savanna areas; 3) Mopane Savanna and Thornbush Savanna areas; 4) Highland Savanna; and, 5) Northern and Central Kalahari Desert and Karstveld areas. As can be seen in figure 4, there is a definite west to east gradient which reflects the climatic, vegetational, and geological differences in these areas (Coetzee 1983; Giess 1971).

Principle components analysis

The PCA, using 38 species (10 species could not be used because they were represented in only one locality each) as variables, was able to extract 33 principle axes. The first axis accounts for 15.3 % of the total variation. The second and third axes account for 9.4 % and 7.7 % of the variation, respectively. The first ten axes are necessary to represent 70 % of the variation. This indicates that the total variation is spred over almost all of the species distributions more or less equally. However, certain patterns can be recognized using the first axis alone.

As can be seen in figure 5, Principal Component (PC) I appears to be an east/west component. Low PC scores for the pooled localities occur in the west and south while high PC scores occur in the northeast. The distribution of PC scores corresponds with the distribution of clusters as discussed previously. Rainfall increases from west to east and south to north in Namibia (Coetzee 1983; Giess 1971). This would indicate that the First Principal Component is related to the ecological distribution of various species.

The distribution of representative high and low "loading" species on PC I are shown in figure 6. Species (variables) in this analysis had PC loading coefficients (Tab. 3) ranging from −0.61 (*Petromus typicus*) to +0.79 (*Mastomys natalensis*). Species with negative loading coefficients tend to be in the west and south while those with positive loading coefficients are in the northeast.

As we interpret these results, species with very low (negative) PC loading are more arid adapted while those with very high (positive) PC loading are more mesic. Species with low

Table 2. **Checklist of species**

Species names followed by a list of locality numbers from table 1

INSECTIVORA

1. *Crocidura cyanea* – 36, 40, 50, 55, 56, 57, 65.
2. *Crocidura fuscomurina* – 14, 29, 32, 38.
3. *Crocidura hirta* – 13, 14, 35, 37, 38, 46.
4. *Crocidura mariquensis* – 20.

MACROSCELIDEA

5. *Macroscelides proboscideus* 5 43, 61.
6. *Elephantulus intufi* – 1, 9, 14, 16, 18, 22, 24, 26, 27, 28, 29, 30, 32, 34, 35, 36, 37, 38, 40, 41, 46, 47, 48, 51, 54, 55, 59, 60, 65, 70.
7. *Elephantulus rupestris* – 9, 16, 39, 43, 44, 50, 55, 57, 58, 59, 67, 68, 72.

LAGOMORPHA

8. *Lepus capensis* – 10, 37, 39, 41, 44, 46, 47, 48, 56, 62, 66, 73.
9. *Lepus saxatilis* – 2, 12, 35, 40, 41, 46, 47, 48, 65, 68, 72.
10. *Pronolagus randensis* – 47.

RODENTIA

11. *Cryptomys hottentotus* – 6, 8, 9, 12, 14, 41, 42, 45, 48, 52.
12. *Hystrix africaeaustralis* – 40, 41, 46.
13. *Pedetes capensis* – 2, 10, 12, 13, 14, 16, 26, 29, 32, 34, 35, 37, 38, 39, 40, 41, 42, 47, 48, 51, 53, 55, 56, 63, 66, 68, 69, 73.
14. *Graphiurus murinus* – 12, 14, 26, 34, 53.
15. *Graphiurus platyops* – 44.
16. *Xerus inauris* – 16, 24, 32, 35, 41, 42, 46, 51, 55, 56, 58, 65, 66, 69, 72, 73.
17. *Funisciurus congicus* – 2, 15, 17, 20.
18. *Paraxerus cepapi* – 13, 17, 20.
19. *Petromus typicus* – 5, 40, 47, 50, 55, 57, 65, 67, 73.
20. *Parotomys brantsii* – 66, 69.
21. *Parotomys littledalei* – 49, 64, 65.
22. *Lemniscomys rosalia* – 6, 10, 14, 26, 27, 28, 31.
23. *Rhabdomys pumilio* – 25, 28, 36, 37, 40, 41, 43, 46, 47, 49, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 62, 64, 65, 66, 67, 68, 69, 70, 72, 73.
24. *Zelotomys woosnami* – 26, 38.
25. *Mus indutus* – 4, 6, 8, 13, 14, 16, 19, 20, 23, 26, 27, 28, 29, 30, 32, 33, 34, 35, 36, 37, 38, 40, 41, 42, 46, 47, 48, 49, 50, 51, 54, 55, 56, 65, 66.
26. *Mus minutoides* – 8, 12, 37.
27. *Mus setzeri* – 12.
28. *Mastomys natalensis* – 4, 6, 8, 10, 11, 12, 13, 14, 16, 17, 19, 20, 22, 23, 24, 26, 27, 28, 30, 31, 32, 34, 35, 36, 37, 38, 40, 41, 42, 46, 49, 51, 52, 56.
29. *Mastomys shortridgei* – 20.
30. *Thallomys paedulcus* – 4, 6, 10, 13, 14, 15, 30, 34, 36, 40, 42, 47, 48, 55, 57, 59, 65, 66.
31. *Aethomys chrysophilus* – 1, 6, 8, 10, 11, 13, 14, 16, 17, 19, 24, 27, 29, 31, 32, 35, 37, 38, 41, 46, 50, 55.
32. *Aethomys namaquensis* – 1, 2, 3, 5, 7, 13, 16, 17, 20, 21, 22, 23, 24, 27, 28, 29, 30, 31, 34, 36, 37, 38, 39, 40, 41, 42, 43, 44, 46, 47, 48, 50, 51, 52, 54, 55, 56, 57, 58, 59, 60, 65, 67, 68, 72, 73.
33. *Desmodillus auricularis* – 5, 32, 35, 51, 62, 64, 65, 66, 73.
34. *Gerbillurus paeba* – 5, 12, 13, 24, 25, 29, 30, 31, 32, 35, 38, 39, 40, 41, 42, 43, 44, 47, 49, 51, 56, 58, 60, 64, 66, 68, 69, 71, 73.
35. *Gerbillurus setzeri* – 40.
36. *Gerbillurus tytonis* – 64.
37. *Gerbillurus vallinus* – 70.
38. *Tatera leucogaster* – 1, 2, 5, 6, 8, 10, 11, 12, 13, 14, 15, 16, 19, 20, 22, 23, 24, 27, 28, 29, 30, 32, 33, 34, 35, 37, 40, 41, 42, 43, 46, 47, 50, 51, 53, 55, 56, 58, 66, 69, 72.
39. *Tatera brantsii* – 31, 56, 66.
40. *Saccostomus campestris* – 6, 10, 12, 13, 14, 16, 22, 23, 26, 28, 29, 30, 32, 34, 35, 37, 38, 39, 40, 41, 47, 51, 52, 56.
41. *Malacothrix typica* – 16, 37, 42, 51, 55, 56, 65.
42. *Dendromus melanotis* – 12, 26, 31, 41, 46.
43. *Steatomys parvus* – 12.
44. *Steatomys pratensis* – 10, 14, 16, 26, 27, 28, 29, 41, 50, 55, 64.
45. *Petromyscus collinus* – 5, 7, 21, 22, 28, 39, 40, 44, 50, 57, 58, 67.
46. *Petromyscus monticularis* – 65.

HYRACOIDEA

47. *Procavia capensis* – 40, 51, 56, 65, 72, 73.
48. *Procavia weltwitschii* – 3, 5.

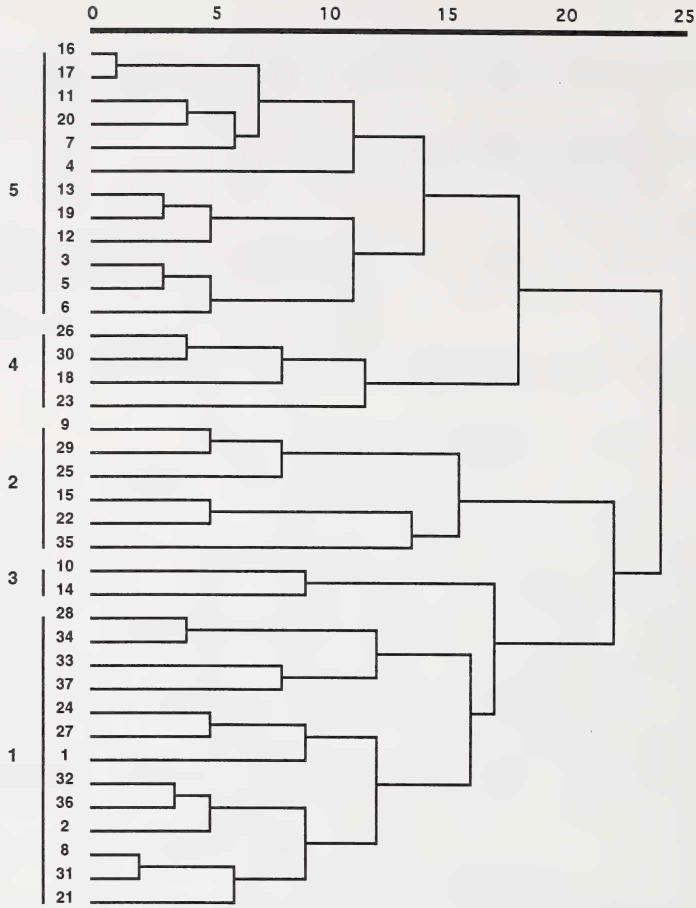

Fig. 2. Dendrogram of pooled localities showing recognized clusters. Numbers of minor clusters on the left. Major Cluster I includes 1, 2, and 3. Major Cluster II includes 4 and 5. See text for explanation

PC loadings include *Petromus typicus* (−0.61). *Elephantulus rupestris* (−0.56), *Petromyscus collinus* (−0.56), and *Rhabdomys pumilio* (−0.54). RAUTENBACH (1978) indicated that the first three of these species were restricted to the Southwest Arid and/or Namib Desert Biotic Zones. Species with high PC loadings include *Mastomys natalensis* (+0.79), *Aethomys chrysophilus* (+0.73), *Saccostomus campestris* (+0.72), and *Crocidura hirta* (+0.54). These species, while occurring in the Southwest Arid Biotic Zone, are also found in more mesic regions (RAUTENBACH 1978).

When the results of both the Cluster and PC analyses are considered together, the distribution patterns of small mammals are more clear. Cluster 1 (Fig. 3) represents the arid west and south of Namibia. Low PC scores for localities in these areas support this idea (Fig. 5), as well as, the low PC loadings for species (Fig. 6) that are considered to be restricted to arid regions. These species have a major portion of their distribution in the localities of Cluster I. Cluster II (Fig. 3) represents localities in the north and east of Namibia and have relatively high PC scores (Fig. 5). The species associated with this cluster are those with positive loadings and a more mesic ecological distribution.

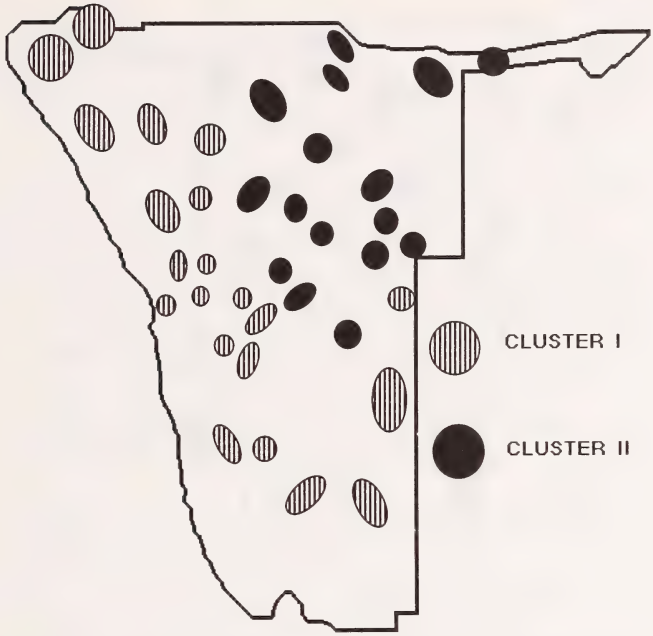

Fig. 3. Map of Namibia showing distribution of two major clusters

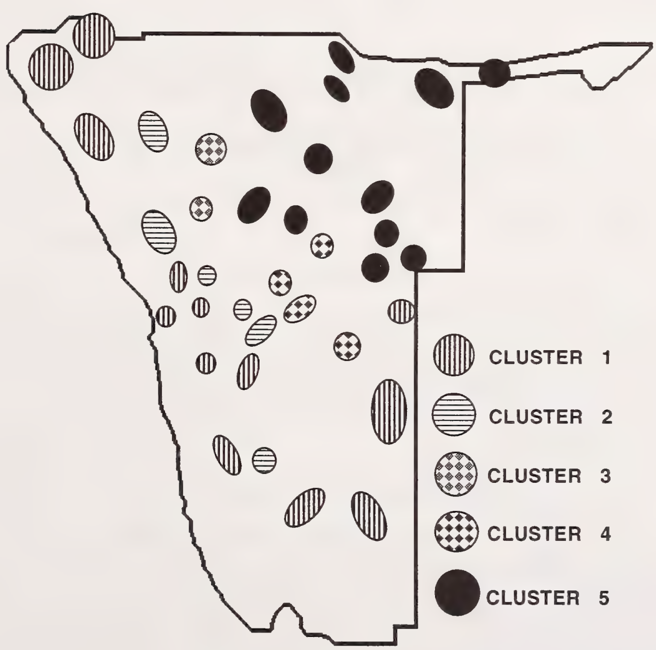

Fig. 4. Map of Namibia showing distribution of five minor clusters corresponding to vegetation and biotic areas. See text for explanation

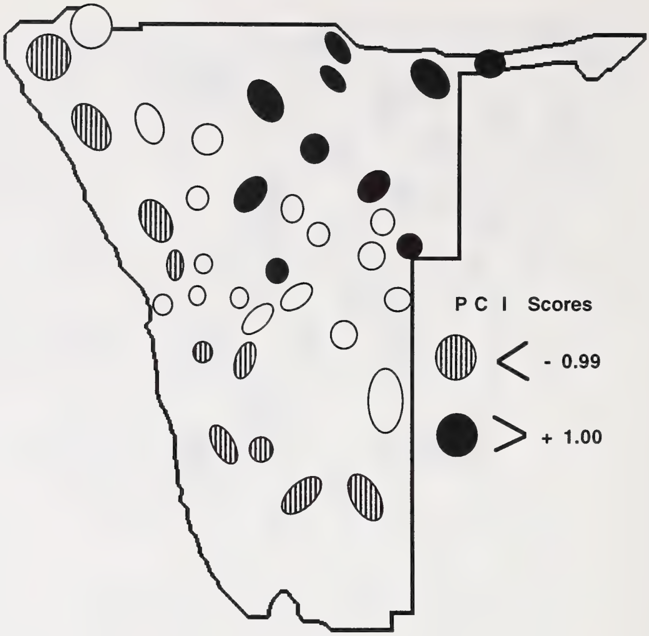

Fig. 5. Map of Namibia showing distribution of high and low PC scores for each pooled locality

Localities within Namibia that have intermediate PC scores contain a mixture of species. In addition, those species with intermediate loadings (between +/−0.50) are either widely distributed or have few locality records. Widely distributed species include *Gerbillurus paeba* (PC loading of 0.00 and occurring in 23 of the 37 pooled localities). Species with few locality records include *Parotomys littledalei* (PC loading of −0.31 and

Table 3. **First Principal Component loading coefficients for 38 species of small mammals in Namibia**

Coefficient/Species		Coefficient/Species	
–0.61	*Petromus typicus*	+0.11	*Paraxerus cepapi*
–0.56	*Elephantulus rupestris*	+0.13	*Mastomys shortridgei*
–0.56	*Petromyscus collinus*	+0.21	*Tatera leucogaster*
–0.54	*Rhabdomys pumilio*	+0.23	*Tatera brantsii*
–0.34	*Crocidura cyanea*	+0.25	*Elephantulus intufi*
–0.31	*Parotomys littledalei*	+0.28	*Mus minutoides*
–0.30	*Aethomys namaquensis*	+0.32	*Steatomys pratensis*
–0.28	*Procavia capensis*	+0.37	*Zelotomys woosnami*
–0.27	*Desmodillus auricularis*	+0.40	*Graphiurus murinus*
–0.25	*Macroscelides proboscideus*	+0.45	*Cryptomys hottentotus*
–0.21	*Procavia welwitschii*	+0.45	*Dendromus melanotis*
–0.13	*Lepus saxatilis*	+0.47	*Crocidura fuscomurina*
–0.07	*Xerus inauris*	+0.48	*Pedetes capensis*
–0.05	*Thallomys paedulcus*	+0.50	*Lemniscomys rosalia*
–0.04	*Funisciurus congicus*	+0.50	*Mus indutus*
–0.03	*Malacothrix typica*	+0.54	*Crocidura hirta*
–0.03	*Lepus capensis*	+0.72	*Saccostomus campestris*
–0.00	*Gerbillurus paeba*	+0.73	*Aethomys chrysophilus*
+0.09	*Hystrix africaeaustralis*	+0.79	*Mastomys natalensis*

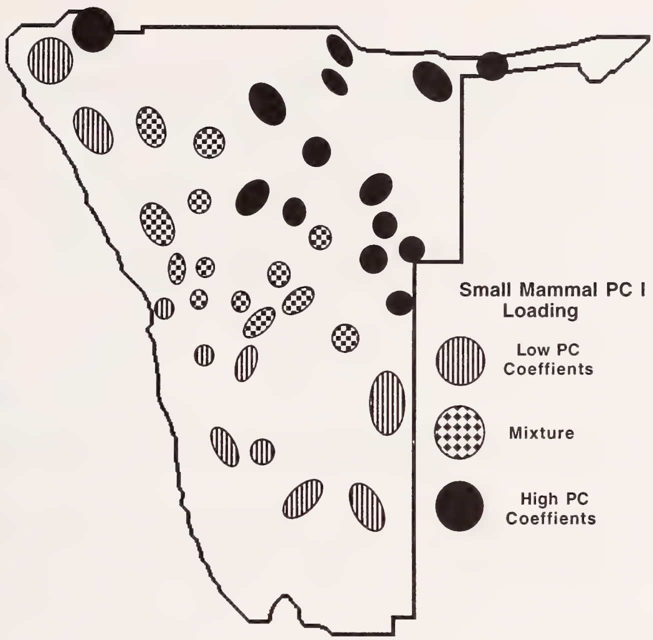

Fig. 6. Map of Namibia showing distribution of small mammal species that have high or low loading coefficients on the First Principal Component. See text and table 2 for species and explanation

found in only three localities of Cluster I) and *Zelotomys woosnami* (PC loading of +0.37 but found in only two localities of Cluster II).

While these results are based only upon a sample of the mammals from Namibia, they do reveal trends similar to those described by Coetzee (1983) and Rautenbach (1978). Bigalke (1972) and Morain (1984) considered southwestern Africa (including Namibia, parts of Botswana, and most of South Africa) to be an important biogeographic region because of the high amount of endemism. While our analyses would appear to represent more of an ecological distribution, it does confirm the zoogeographic analyses of Coetzee (1983) and Rautenbach (1978).

Acknowledgements

We thank John Heyning, Sarah George, and Linda Barkley of the LACM for allowing us to work with the Namibia Mammal Collection. A major portion of this collection was aquired through the efforts of Lani Lester. The original expedition, October and November 1972, and a 1974 expedition were sponsored by Mrs. Reese Taylor. Additional specimens were obtained between 1974 and 1977. Travel funds to visit the LACM were made available through a San Jose State University Foundation, Faculty Development Grant and the Department of Biological Sciences, San Jose State University.

Zusammenfassung

Verbreitungsmuster von Kleinsäugern in Namibia

Eine Sammlung von über 6500 Kleinsäugern aus Namibia wurde genutzt, um ökologische und zoogeographische Verbreitungsmuster zu ermitteln. Über das ganze Land verteilte Einzellokalitäten wurden zu 37 Fundgebieten zusammengefaßt. Multivariate Auswertungstechniken (Cluster Analysis, Principal Components Analysis) ergaben klare ökologische Verbreitungsmuster, die den Klima- und Vegetationstypen von Namibia folgen. Fünf ökologische Hauptregionen lassen sich definieren, die mit bereits von früheren Autoren charakterisierten Vegetationszonen und zoogeographischen Regionen korrespondieren.

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Authors' addresses: John O. Matson, Department of Biological Sciences, San Jose State University, San Jose, CA 95192 and Brad R. Blood, Department of Physical Therapy, Mt. St. Mary's College, Los Angeles, CA 90049, USA

Z. Säugetierkunde 59 (1994) 299–308
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ISSN 0044-3468

Cytogenetic diversity and evolution of Andean species of *Eligmodontia* (Rodentia, Muridae)

By A. E. Spotorno, J. Sufan-Catalan, and Laura I. Walker

Laboratorio de Citogenética Evolutiva, Departamento de Biología Celular y Genética, Facultad de Medicina, Universidad de Chile, Santiago, Chile

Receipt of Ms. 4. 2. 1994
Acceptance of Ms. 31. 5. 1994

Abstract

The standard and G-banded chromosomes of northern species of the phyllotine genus *Eligmodontia* were investigated. *E. puerulus* showed 2n = 50, NFa = 48 in bone marrow cells of three males and four females from northern Chile, and *E. moreni* 2n = 34, NFa = 48 in three males from northern Argentina. Comparisons showed extensive conservation of G-band patterns, including those of 15 telocentric chromosomes of the former with the arms of eight metacentrics of the latter; these characteristics suggest seven centric fusions and one pericentric inversion in *E. moreni*. C-bands were small in *E. puerulus*, as well as in the related *Andinomys edax* 2n = 54, NFa = 54 (two males and one female from northern Chile). All these northern species have chromosome arm sizes smaller than 9 % of the total karyotype, in contrast to some longer arms reported in the southern *E. typus* and *E. morgani*; the latter were probably derived by tandem fusions. Thus, southern species comprise a derived phyletic line, probably evolved from a primitive northern ancestor having 2n = 50 and NFa = 48. The role of geographic and cytogenetic factors in this speciation pattern, similar to that of the related *Auliscomys* species living in the same area, is discussed.

Introduction

Among the nine genera included in the tribe Phyllotini of South American murid rodents, *Eligmodontia* is clearly distinct and specialized, given its adaptations to life in arid zones. Although it was considered monotypic by some authors, two recent cytogenetic studies (Ortells et al. 1989; Kelt et al. 1991) support the idea that at least three species should be distinguished, on the basis of striking chromosomal differences. These are: *Eligmodontia puerulus*, 2 n = 50, NFa = 48 (Pearson and Patton 1976; Ortells et al. 1989), reported for populations living in the Altiplano (the highlands of southern Peru, Bolivia and northern Argentina); *E. typus*, 2n = 44, NFa = 44 (Ortells et al. 1989) for populations from central Argentina; and *E. morgani*, 2n = 32, NFa = 32 (Ortells et al. 1989; Kelt et al. 1991) for those from southern Argentina. A cytologically unknown fourth species from northern Argentina, *E. moreni*, has also been included in the most recent world species list (Musser and Carleton 1993), but these authors stated (p. 701) that "The differentiation of *moreni* from *morgani* in the S Andes and from *typus* in the Pampas warrants further study".

We present here cytogenetic data on specimens of this fourth species. We also compare all standard chromosomes described for these four species, as well as the G-banded karyotypes of *Eligmodontia puerulus* from northern Chile and *E. moreni* from northern Argentina. In addition, we present C banded karyotypes of the first species and those of the karyotypically related phyllotine *Andinomys*, both from northern Chile, to date not yet described in these terms. The latter is a monotypic genus of the Altiplano, considered to be primitive on the basis of protein electrophoresis (Spotorno 1986).

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Material and methods

Specimens

All animals were collected in the field. Skulls and skins were prepared as voucher specimens and deposited in the collection of the Laboratorio de Citogenética, Facultad de Medicina, Universidad de Chile (LCM).

Taxa (taxonomic names according to MUSSER and CARLETON 1993), original localities, number and sex of specimens (LCM numbers in parenthesis) were as follows. *E. puerulus*: Parinacota, 110 km NE Arica, I Región de Tarapacá, CHILE, 1 male (LCM 650); Choquelimpie, 114 km NE Arica, I Región de Tarapacá, CHILE, 2 males (LCM 1183–1193) and 4 females (LCM 1184–1283–1438–1439). *E. moreni*: Cauchari, Provincia de Salta, ARGENTINA, 3 males (LCM 1702–1703–1704). *Andinomys edax*: Murmuntani, 110 km E Arica, I Región de Tarapacá, Chile, 1 male (LCM 243); Pampa Yuscuni, 100 km NE Arica, I Región de Tarapacá, Chile, 1 male and 1 female (LCM 678–677).

Chromosome analysis

Chromosomes were obtained from bone marrow cells using the conventional in vivo colchicine hypotonic technique, preceded by a yeast injection to improve the mitotic index (LEE and ELDER 1980). Total chromosome counts per cell were made in at least five good quality metaphases per specimen. NFa is the number of visible autosomal arms per cell.

Chromosome measurements were based on photographic enlargements, using the best single chromatid per pair (best meaning easiest to measure). Values were transformed to percentages of the total haploid female set. Relative values, together with those from idiograms already published, were displayed in a scatter diagram, which we have called the karyo-idiogram (SPOTORNO et al. 1987); each chromosome is represented by a single point according to its arm lengths. This is a useful device which allows the simultaneous description, comparison and eventual distinction of all chromosomes from many species. Two derived morphological variables can be evaluated: total chromosome size (short arm plus long arm lengths) and centromeric index (100 times short arm length divided by total chromosome length). Such a procedure assumes that the total genome size is conserved among the species compared. Although this assumption is generally true for mammals, it may be validated by C-banding techniques, which detect heterochromatin-containing satellite DNA, or by the use of marker chromosomes when available (SPOTORNO et al. 1987).

Chromosomes were classified according to morphology (centromere position) using the nomenclature of LEVAN et al. (1964), and also according to size. We distinguished large, medium or small chromosomes when their relative lengths were > 9 %, 9–5.5 % or < 5.5 % of the female haploid set, respectively (see MASSARINI et al. 1991).

Chromosome bands were obtained by treating metaphase cells with G-banding (CHIARELLI et al. 1972) and C-banding techniques (CROSSEN 1972; SUMNER 1972). Comparisons of G-banded karyotypes were made in at least three selected metaphases from each taxon. Using shared G-band patterns, chromosomes from two or more species were classified as totally corresponding, partially corresponding or unique (WALKER et al. 1979).

Results

The karyotypes of the two main geographic populations were clearly different. All the specimens of *E. puerulus* from Chile exhibited cells with 2n = 50 and NFa = 48. All chromosomes were telocentric, with no visible short arms (Fig. 1a). This karyotype was essentially identical to those described for populations from Peru, Bolivia and northern Argentina (ORTELLS et al. 1989; KELT et al. 1991). Chromosome sizes graded from medium to small. The largest telocentric chromosome (pair 1) was clearly identified by size, amounting to 8.3 % of the total karyotype length. Pairs 3 and 8 showed a secondary constriction in the middle of their long arms (arrows in Fig. 1a), although the latter was not clearly visible in short metaphases. Sex chromosomes were difficult to identify in standard Giemsa karyotypes; the X was the third largest and the Y was among the many small chromosomes.

All the *Eligmodontia moreni* specimens from northern Argentina consistently showed karyotypes with 2n = 34 and NFa = 48 (Fig. 1b). The eight largest chromosomes displayed metacentric or submetacentric shapes, with pairs 3 and 6 exhibiting a clear secondary

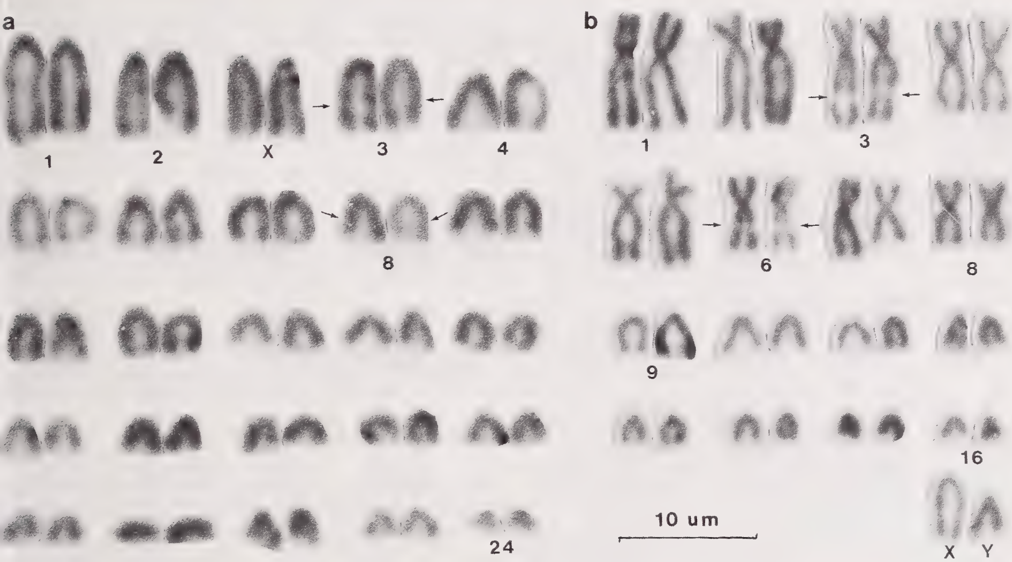

Fig. 1. Standard karyotypes of: a) *Eligmodontia puerulus* female (LCM 1193), X chromosome localized according to its size; and b) *E. moreni* male (LCM 1704). Arrows point to secondary constrictions

constriction in the middle of their long arms (arrows in Fig. 1b). The largest chromosome arm comprised 8.5 % of the karyotype length. The X chromosome was the largest telocentric, and the Y a small telocentric with an extremely short arm.

G-bands allowed the identification and comparison of every chromosome from both karyotypes. The X of *E. puerulus* was the third in size (Fig. 2a), showing two dark bands in the middle of its arm, a pattern already described for most mammals (Pathak and Stock 1974). It was almost identical to the X of *E. moreni* (Figs. 2b and 3). The Y chromosomes from both species were also very similar in bands and size, except for the presence of a short arm unique to *E. moreni* (Fig. 3).

When G-banded karyotypes were compared side by side (Fig. 3), all chromosomes or chromosome arms were found to correspond in bands and sizes. The single exception was chromosome 13 from *E. puerulus*, which appears to be unique. In particular, the arms of the largest seven metacentric chromosomes of *E. moreni* had corresponding telocentric chromosomes in *E. puerulus*, suggesting the occurrence of Robertsonian fusion/fission processes during the evolution of these species. The remaining metacentric pair 8 corresponded in bands and size to the single telocentric pair 5 from *E. puerulus*, suggesting the occurrence of a pericentric inversion.

C-bands were very small and confined to centromeric positions in most, if not all, the chromosomes of both *E. puerulus* (Fig. 4a) and *Andinomys edax* (2n = 56, NFa = 56, Fig. 4b). The latter karyotype was very similar to that reported for a single female from northern Argentina (Pearson and Patton 1976), with the exception that only pairs 1, 27 and Y had short arms in these Chilean specimens. A faint intercalar C-band was observed in the middle of pair 8 in *Andinomys*, and at a similar site of pair 3, or perhaps 4, in *E. puerulus*; this happens to be the usual localization of secondary constrictions in its Giemsa standard chromosomes (Fig. 1a).

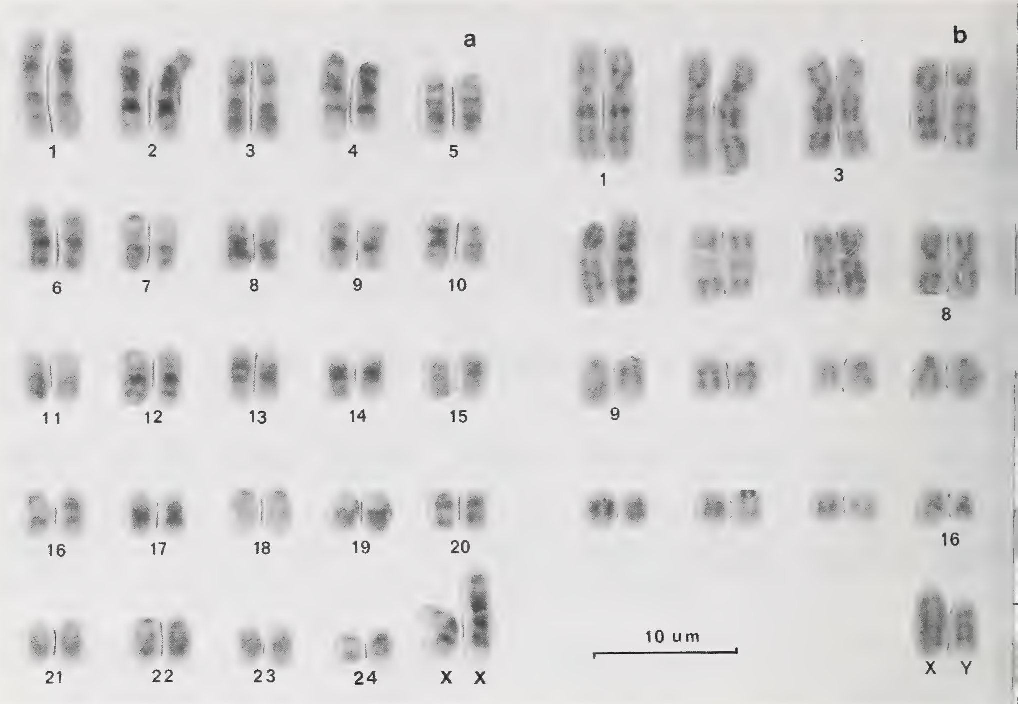

Fig. 2. G-banded karyotypes of: a) *Eligmodontia puerulus* female (LCM 1283); and b) *E. moreni* male (LCM 1704). Arrows point to secondary constrictions

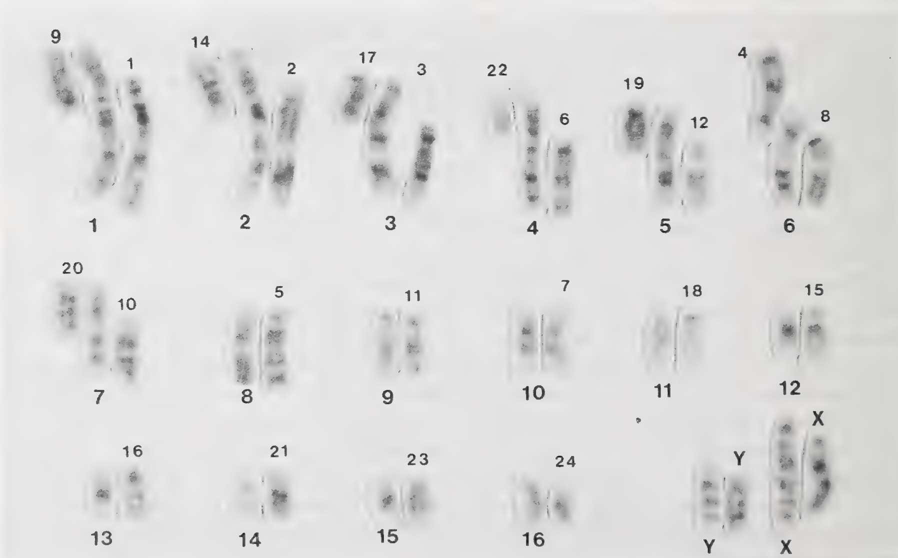

Fig. 3. Correspondence of G-band patterns between the chromosomes of *Eligmodontia moreni* (aligned large numbers at bottom) and *E. puerulus* (small numbers above). Chromosome 13 of the former not included, since it was difficult to match

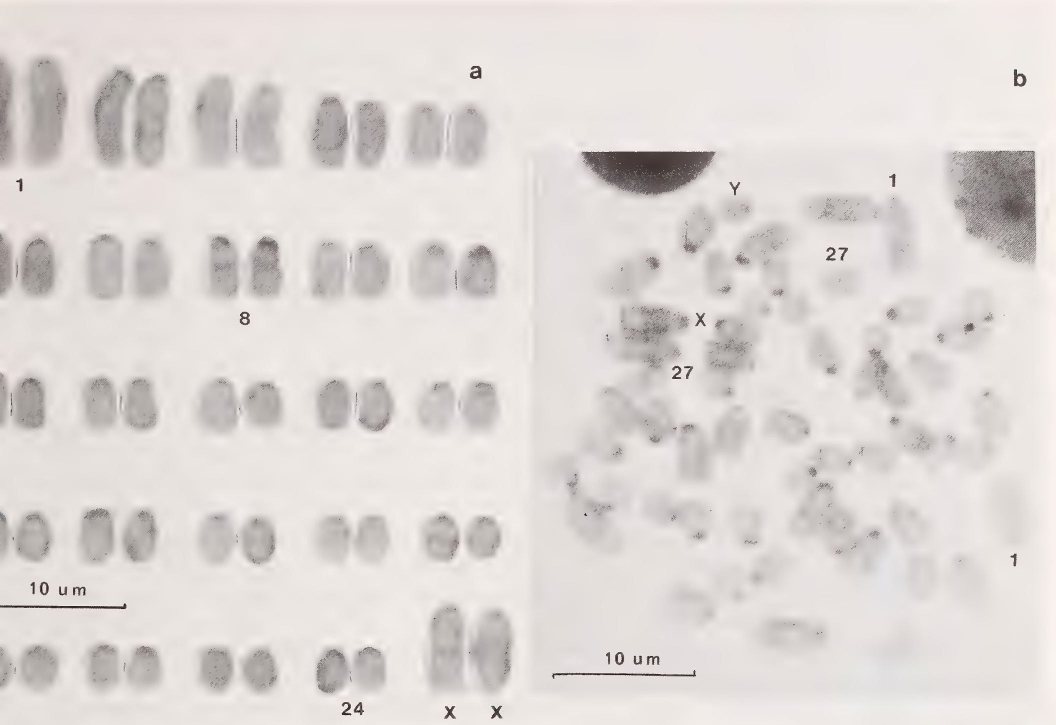

Fig. 4. C-banded metaphases of: a) *Eligmodontia puerulus* female (LCM 1283), and b) *Andinomys edax* male (LCM 678), with 2n = 56, NFa = 56. Sex chromosomes and the smallest metacentric autosome are indicated

Discussion

Our results provide data allowing for a reasonably complete view of the extreme cytogenetic diversity and the still obscure phylogenetic relationships of *Eligmodontia* species.

But firstly, we will now evaluate empirically the assumption that, despite the large changes in 2n and NFa, the total genome sizes of *Eligmodontia* species have been conserved since their last common ancestor. On the one hand, there are no large amounts of heterochromatin in *E. puerulus* NFa = 48, or in *E. typus* NFa = 44 (Ortells et al. 1989), or in the related phyllotine *Andinomys edax* NFa = 56. On the other hand, if relative lengths of all chromosomes from the five species are compared in a single karyo-idiogram, as shown in figure 5, at least two marker chromosomes, the X and Y, clearly retain their relative lengths at roughly 6 to 7% and 3.4 to 3.9%, respectively, despite the most probable pericentric inversion which gave rise to the derived *typus* X and Y, as well as the *morgani* Y chromosome. If large changes in total genome size had occurred, such length ranges should be expected to exhibit larger variations than those observed here. G-bands, where available, also document the size constancy of the identified sex chromosomes. In summary, gross constancy among genome sizes may be accepted as a reasonable assumption for further chromosome comparisons based on relative lengths.

Inferences about species distinctions, chromosomal changes and phylogenetic relationships can be made from our results when compared with those already published. It is immediately obvious that at least seven Robertsonian fissions or fusions and one pericen-

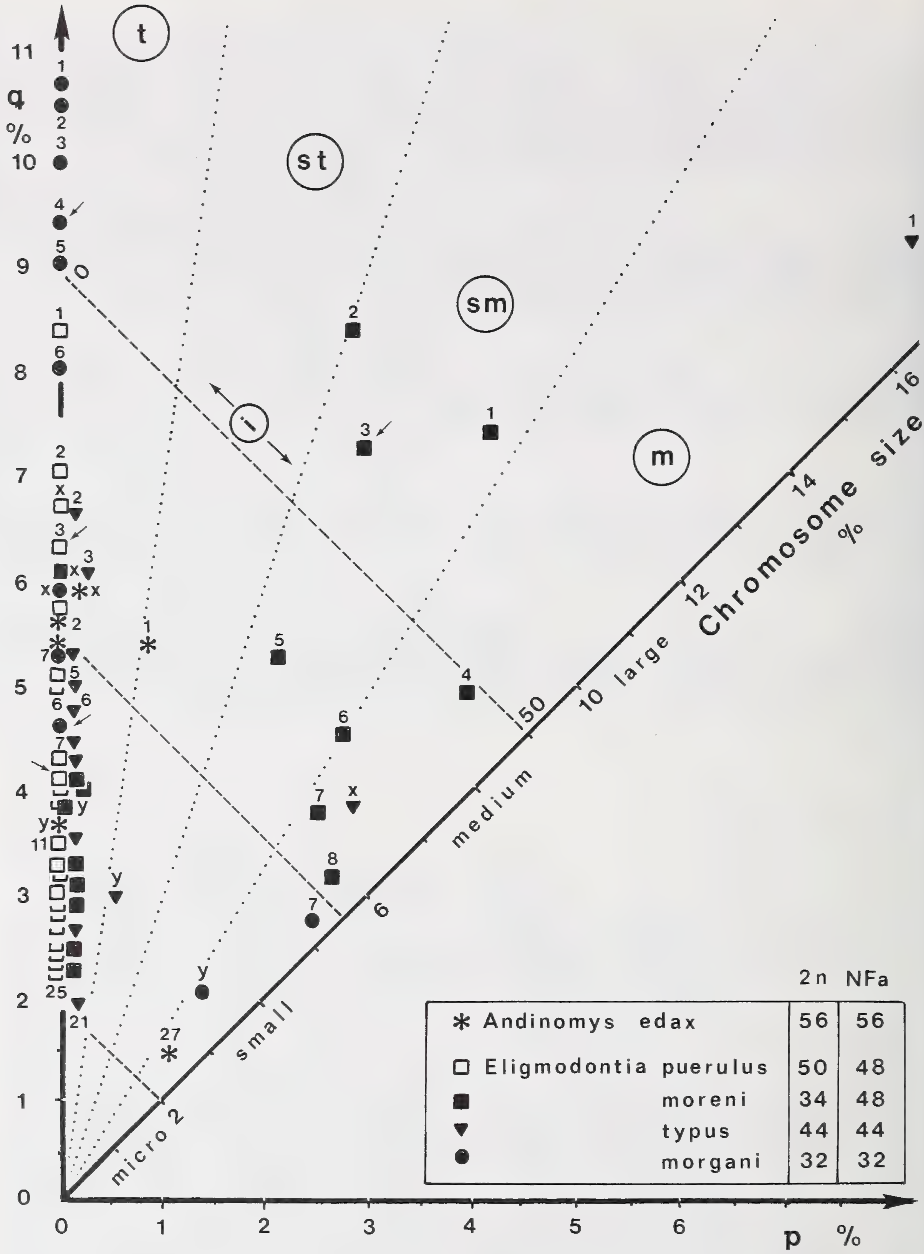

Fig. 5. Karyo-idiogram (bivariate plot) showing relative sizes of short arm (p) versus long arm (q) chromosomes from four *Eligmodontia* species and *Andinomys* (not all chromosomes actually shown). Total chromosome size may be read on the diagonal; chromosome classifications by morphology and size follow LEVAN et al. (1964) and ORTELLS et al. (1989), respectively. *Eligmodontia typus* and *E. morgani* data are from ORTELLS et al. (1989)

tric inversion strongly support the separate species status of *E. puerulus* and *E. moreni*. The eventual hybrid produced from a cross among individuals with such karyotypes most probably would exhibit abnormal meiosis and reduced fertility. Therefore, the chromosome differences detected substantiate the morphological and ecological distinctions previously noted between populations of both nominal species (Mares et al. 1989).

At the same time, the NFa = 48 shared only by these two species suggests a primitive condition close to the NFa = 54 shown by *Andinomys*. These three species with only medium or small chromosomes (see Fig. 5) have in fact close and exclusive geographic ranges in the Altiplano, and within the northeastern side of the xeric diagonal which divides South America in two parts (Spotorno and Veloso (1989). This geographic subregion has been considered the center of origin of the phyllotine group (Reig 1986). Independent evidence based on electrophoretic analysis of proteins also placed the monotypic *Andinomys* at the base of the phyllotine radiation (Spotorno 1986).

The southernly distributed *E. typus* and *E. morgani* seem to belong to a different and derived phyletic line. Their divergent karyotypes NFa = 44 and 32 are characterized by chromosome arms longer than 9 %, which are absent in the NFa = 48 karyotypes: the long arm of *E. typus* metacentric pair 1 and the long arms of *E. morgani* telocentric pairs 1 through 5 (Fig. 5). These have been interpreted as being produced by tandem translocations (Ortells et al. 1989). As such, they must represent derived conditions that arose from the primitive ones presently seen in the northern NFa = 48 karyotypes.

For instance, chromosome comparisons based on the karyo-idiogram (Fig. 5) allow the proposal of the following most simple transformation series. The largest metacentric pair 1 of *E. typus*, having arms of 9.3 and 8.2 %, is surely a unique and extremely derived condition. It was probably formed from the centric fusion of two derived telocentric elements of correspondant large sizes, similar to pairs 5 and 6 of *E. morgani* (pair 5 being the intermediate condition shared by *E. typus*). Finally, the derived large telocentric *morgani* chromosome 5 probably arose through tandem fusion of two small telocentric elements such as those found in *E. puerulus* (the most ancestral condition, also shared by *Andinomys*), or in the small q arm of metacentric 1 of *E. moreni* (an additionally derived condition). Such a transformation series for this character may be linearly written through the following species tree: *([typus, morgani] puerulus [moreni])*. This topology is also a reasonable summary of cytogenetic data, as well as of geographic data, since it is consistent with the southern (*typus-morgani*) – northern (*puerulus-moreni*) axis of species distribution; therefore, it is a good candidate for a reasonable estimate of the real species phylogeny.

A strikingly similar northern-southern geographic pattern has been postulated for the chromosomal evolution of four related phyllotine species of the genus *Auliscomys* (Walker and Spotorno 1993). Among them, "an ancestral telocentric karyotype would have undergone three consecutive tandem fusions" in southern species; later, three centric fusions probably occurred in northern species. The paleogeographic model proposed there, based on the assumption that actual biotic patterns in South America were determined by Quaternary geological and climatic changes (Vuillemier 1971), seems to be also valid for *Eligmodontia* species.

Moreover, the extreme cytogenetic diversity of *Eligmodontia*, as well as the occurrence of tandem fusions rarely documented in mammals, suggest an active role of chromosomal changes in the speciation process. Although this has been a subject of renewed interest and controversy (Capanna 1982; Patton and Sherwood 1983; Baker and Bickham 1986; Sites and Moritz 1987), recently Reig (1989) has contributed importantly to clarify such causal relationship; he suggested that explosive speciation processes were triggered by chromosomal rearrangements. However, fertility studies on the heterozygotes for different chromosomal rearrangements indicate that meiotic and evolutionary consequences are drastically different, depending upon the type of rearrangement. Thus, while single centric

fusions would have little or no reproductive isolation effects, because the fertility of heterozygotes is modified slightly or not at all (Bickham and Baker 1979; John 1981; Patton and Sherwood 1983), single tandem fusions would have drastic consequences, severely reducing the fertility of heterozygotes (White 1973; John 1981; for a recently reported case where tandem fusions are involved in hybrid infertility, see Ryder et al. 1989). The fact that both types of chromosomal changes have occurred independently within two different but related phyletic lines evolving within the same subregions, invites consideration of geographic factors in contrast to cytogenetic factors.

The following hypothetical sequence of events would be consistent with our cytogenetic data, the present species ranges and geography of the region. An ancestral, perhaps late Miocene species with NFa = 48, having a wide northern-southern range, was separated by the Plio-Pleistocene xeric diagonal. The northern ancestor would have evolved into the present *E. puerulus*, maintaining its karyotype morphology, and secondarily to *E. moreni*, mainly by centric fusions. Here, the ice barriers generated by cyclic glacial warming and freezing within the Andean valleys (Vuillemier 1971) would be an associated requirement for speciation processes that maintained the NFa = 48; i.e. geographic factors would be sufficient for biological isolation, and cytogenetic isolation was not required. By contrast, the populations on the flat landscapes of southern Argentina were less prone to be affected by such ice barriers. Here, tandem fusions, with drastic meiotic isolating consequences, could probably be sufficient to change NFa. In other words, geographic factors would be insufficient for isolation, and cytogenetic isolation was required in the southern subregion. A similar pattern of chromosome divergence seems to have occurred in the species of *Auliscomys* (Walker and Spotorno 1993). Therefore, the isolation required for speciation might be the product of subsidiary or complementary actions between extrinsic (geographic) factors and intrinsic (chromosome) mechanisms. These would explain the high degree of chromosomal divergence observed among these phyllotine rodents as well as within many mammalian groups.

Acknowledgements

This work was supported by Grant 92-1186 from the Fondo Nacional de Ciencia y Tecnología, Chile. We thank Dr. Luis Contreras and Dr. Pablo Marquette (PSP/WWF 7578 and Lincoln Zoo Neotropical Fund) for providing some field specimens, Mr. German Manríquez for help with German translation and Mr. Juan Oyarce for assistance in the collection and care of the animals.

Zusammenfassung

Cytogenetische Vielfalt und Evolution von Eligmodontia-Arten in den Anden (Rodentia, Muridae)

Bei zwei Arten der Gattung *Eligmodontia* wurden Standard- und G-gebänderte Chromosomen aus Knochenmarkszellen untersucht. Drei Männchen und vier Weibchen von *E. puerulus* aus dem Norden Chiles zeigten 2n = 50, NFa = 48. Drei Männchen von *E. moreni* aus dem Norden Argentiniens zeigten 2n = 34, NFa = 48. Vergleichende Untersuchungen ergaben eine starke Konservierung der G-Bandenmuster. Bei insgesamt 15 telozentrischen Chromosomen von *E. puerulus* stimmten die Bandenmuster mit jenen von 8 metazentrischen Chromosomen von *E. moreni* überein. Dies kann als das Ergebnis von sieben zentrischen Fusionen und einer perizentrischen Inversion bei *E. moreni* interpretiert werden. Ähnlich wie bei der verwandten Art *Andinomys edax* (2n = 54, NFa = 54, zwei Männchen und ein Weibchen aus dem Norden Chiles untersucht), waren die C-Bänder von *E. puerulus* schmal. Im Gegensatz zu den südlichen Arten *E. typus* und *E. morgani* betrugen bei den nördlichen Arten die längsten Chromosomenarme weniger als 9 % des diploiden Karyotyps. Das Auftreten erheblich längerer Chromosomenarme bei den südlichen Arten deutet auf das Vorliegen von Tandemfusionen hin. Die südlichen Arten stellen demnach eine eigene phylogenetische Linie dar, die sich aus einem primitiven nördlichen Vorfahren mit 2n = 50 und NFa = 48 ableitet. Die Bedeutung geographischer und cytogenetischer Faktoren im Artbildungsprozeß bei *Eligmodontia* wird unter Bezugnahme auf *Auliscomys*-Arten aus demselben Verbreitungsgebiet diskutiert.

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Authors' address: Angel E. Spotorno, Juan Sufan-Catalan, and Laura I. Walker, Laboratorio de Citogenética Evolutiva, Departamento de Biología Celular y Genética, Facultad de Medicina, Universidad de Chile, Casilla 70061 – Santiago 7, Chile

Z. Säugetierkunde 59 (1994) 309–316

ISSN 0044-3468

Influence of photoperiod and temperature on moulting processes in *Microtus brandti* (Radde, 1861)

By Annegret Stubbe and Sabine Wiegand

Institute of Zoology, Martin-Luther-University, Halle/Saale, FRG

Receipt of Ms. 29. 1. 1993
Aceptance of Ms. 25. 1. 1994

Abstract

Voles were kept under different environmental conditions (light and temperature regime). The duration of seasonal moults is closely connected with temperature changes. Nevertheless seasonal hair changes seem to be fixed endogenously because they also occur under constant light and temperature conditions. However, the endogenous rhythm can be forced by varying environmental conditions.

An intermediate moult was observed in *Microtus brandti* between the two winter furs. This could be induced by shortening day length. An increase in hair density is a result of short day length and low temperatures.

Introduction

The description of the course of moulting within mammal populations has often led to conflicting information. There is a need to shed some light on these complex processes in populations with regard to age structure and in the consequent differentiation between dependent, so-called mature moults (Stubbe and Wiegand 1994), and seasonal hair changes in adult animals induced by environmental conditions (e.g. day length and temperature alterations, especially). The aim of the present study in the vole *Microtus brandti* was to find a model for the moulting processes not only for the genus *Microtus* but also for small rodents in general.

Material and methods

For species description, animal husbandry and feeding, as well as staining treatment, see Stubbe and Wiegand (1994).

Hair density was determined by a modification of the method of Bake (1966). Six animals were investigated from each maintenance condition (MC). We used samples from the ventral side of winter furs, taking three samples per animal in each case. Pile and guard hairs were counted separately from woolly hairs in an area of 1 mm^2. During the present study the voles were kept under different maintenance conditions (MC):

MC 1: 21 ± 2 °C, L:D = 14:10 (L:D, T = const.)
MC 2: 20 ± 2 °C, L:D adapted to the natural photoperiod (L:D ~, T = const.)
MC 3: T and L:D adapted to the naturally changing conditions (L:D, T ~)
MC 4: 20 ± 2 °C, LL (permanent light).

In addition some data on pelts taken from animals caught between 1988 and 1990 in their natural environment near Ulan-Bator (Mongolia) were analysed.

Results

Seasonal influence on moulting cycles

Under all MC except MC 4 we observed that moults occur throughout the entire year. To assist our understanding, we determined so-called "moulting types" for characteristic hair coat changes of spring- and autumn-born animals (see Tab. 1).

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Table 1. **Moulting types of spring and autumn generation**

Moulting type	Transition from . . . fur into . . . fur Spring generation	Autmn generation
I	first into second juvenile plumage	first insto second juvenile plumage
II	second juvenile into first mature coat (= summer fur)	second juvenile into first mature coat (= winter fur)
III	summer into first winter fur (MC 1: only summer into winter fur)	winter into summer fur
IV	first into second winter fur (missed in MC 1)	summer into winter fur
V	second winter into summer fur (MC 1: winter into summer fur)	

Figure 1 explains the moulting courses of the spring and autumn generations under different MC throughout the year, including moult types. The bars show moult duration, beginning with the earliest, and ending with the latest of all twenty animals investigated at each MC. The different starting points of moulting types I and II are the result of several different birth times.

In spring-born animals we found five moults, whereas voles born in late summer and autumn only showed four hair changes during the first year of life. Moult courses in the spring generation are more complex than those of the autumn generation. Regular overlaps are typical of the spring generation but the moults of autumn-born animals are always temporally separated. Spring-born animals kept under MC 1 only showed four moults,

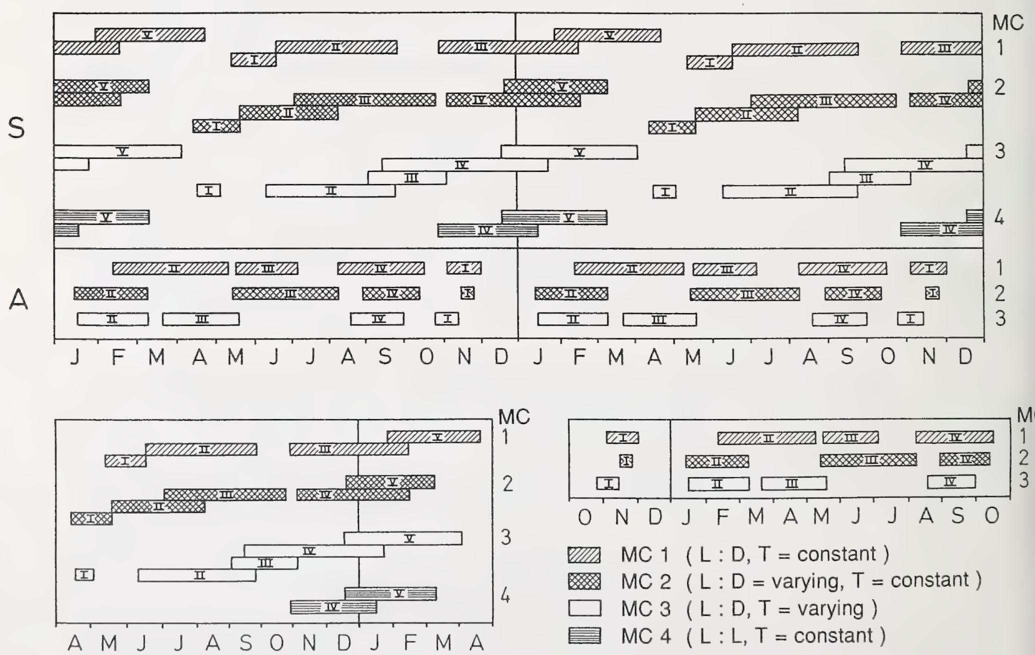

Fig. 1. Moulting courses of spring and autumn generation under different maintenance conditions throughout the year including moulting types

whereas voles under MC 2 and MC 3 passed through five hair changes and developed a second winter pelt.

The duration of the moult into winter fur is abridged, and can be prolonged during the transition from winter into summer coat under the influence of temperature (MC 3) in the spring generation, whereas it is very short in the autumn generation. Under constant conditions (MC 1) we also found a winter and a summer coat. Thus, we can conclude that moulting is fixed endogenously, but influenced by photoperiod and temperature. This opinion is supported by the results of animals kept under permanent light and at constant temperature (MC 4). The moults of these adult voles were only observed for twenty weeks, but they started at the same time as in the animals of MC 1–3 (see Fig. 1).

Duration of moulting

Figure 2 shows the duration of the moult under different MC. The time of change from the first into second juvenile pelage is very short (average 10 days). Most of the time required is in moulting from the second juvenile to the first mature coat (average 40 days). The following seasonal moults (type III–IV) proceed at a faster rate again. Generally the duration of the moult (all moult types) is longer for spring-born animals than for the autumn generation.

Altogether the hair change from the winter to summer fur occurs more rapidly than the stronger temperature-dependent changes from the summer into winter coat (MC 3). Under constant temperature conditions (with or without the influence of photoperiod; MC 1 and MC 2) the moult from summer into winter fur takes longer than the change from the winter into summer coat.

Comparative studies on pelts

Table 2 shows the number of pelts investigated in addition to the observations on living animals and the courses of seasonal moulting under different environmental conditions. All pelts were derived from animals older then 60 days, therefore we found exclusively

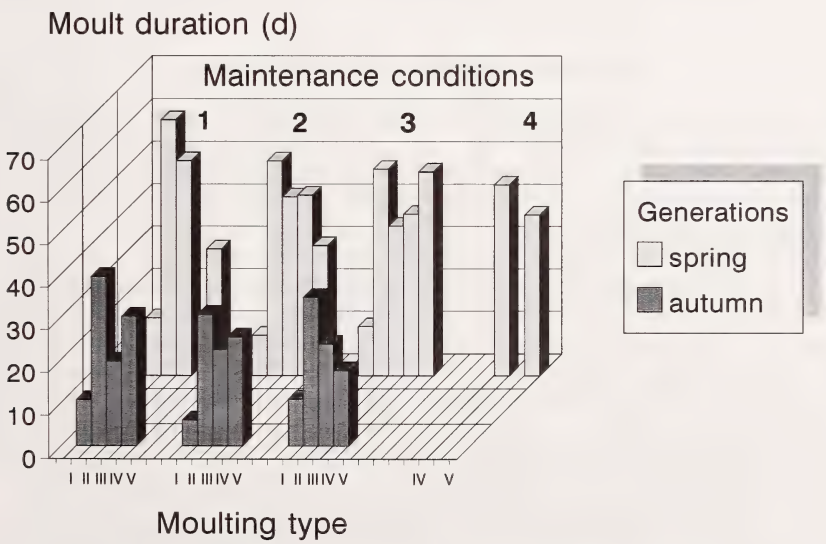

Fig. 2. Average moult duration under different maintenance conditions

Table 2. **Distribution of pelts and moulting patterns throughout the year under different maintenance conditions (MC)**

Month	MC 1 N	MC 1 n (%)	MC 2 N	MC 2 n (%)	W N	W n (%)
January	39	74.4	47	76.6	–	–
February	31	35.5	26	61.5	–	–
March	37	51.4	7	28.6	–	–
April	100	60.0	87	52.9	5	60.0
May	123	69.1	14	57.2	32	65.6
June	55	67.3	4	25.0	23	73.9
July	46	52.2	15	26.7	19	94.7
August	35	74.3	1	0.0	2	0.0
September	112	58.5	16	62.5	12	91.7
October	71	53.5	8	37.5	7	57.1
November	33	45.5	22	77.3	–	–
December	46	69.6	83	92.8	–	–
Total	728	–	330	–	100	–

N = number of pelts investigated; n (%) = percentage of pelts with hair changes; W = pelts of voles caught in the wild (Mongolia).

seasonal moult patterns. Moults appear throughout the year. Under MC 1 the moults were spread comparatively uniformly over several months, showing minimum in February, July, and November. Thus we can assume a slight increase in moulting animals in spring and autumn. However, its induction must be endogenous, because of the absence of any "zeitgeber". Under constant temperature and the influence of photoperiod (MC 2) we found a high percentage of shedding from November to February; the intermediate winter moult occurring at this time. We had no winter pelts from field investigations, so the interpretation of these data is difficult. Normally, the winter coat should be developed at the end of September, and the summer fur at the beginning of June under the extreme conditions of the natural environment; therefore the results in table 2 (W) correspond well with anticipated conclusions. No data are available with regard to a second winter fur of voles living in the steppes of Mongolia.

Hair density dependence on abiotic factors

The results (Tab. 3; 18 samples from six voles under each MC) show an increasing number of hairs from MC 1 to MC 3. There is a significant difference (t-test, $\alpha = 0.05$; Weber 1972) between the number of guard and pile hairs under MC 1 and MC 3, MC 2 and MC 3. The voles kept under the influence of photoperiod and changing seasonal temperatures developed the highest hair densities.

Animals from MC 1 and MC 2 were kept permanently at 20 ± 2 °C. Here, the differences in hair density may be dependent on light conditions. The regulation of fur density could be a primary reaction to temperature alterations, whilst light regime has an accelerating effect. Therefore, hair density may be regarded as an indicator of changes in abiotic factors.

Table 3. **Average number of hairs/mm² and mean variation (winter fur)**

MC	guard and pile hairs	woolly hairs	total hair number
1	9 ± 5	126 ± 26	136 ± 28
2	8 ± 5	134 ± 44	142 ± 47
3	15 ± 5	150 ± 45	165 ± 48

Discussion

Publications commenting on the start and cessation of seasonal moults are rare, de-

scriptions of the course of moulting in whole populations throughout the year being more frequent. Here, the different age classes of animals within populations are rarely considered.

Rowsemitt et al. (1975) described a peak of moulting activity in "autumn" (October until January) and a "spring" moult between June and August in *Microtus breweri* in Massachusetts. Kemper (1976) observed seasonal moults between February and April in *Pseudomys* in Australia, which agrees with the autumn moult of the temperate zone of the northern hemisphere using the same point of time. Bühlow (1970) indicated an increasing proportion of moulting *Arvicola terrestris* in September and again in April. For *Clethrionomys glareolus*, Lehmann (1958) noticed that the highest percentage of moulting animals occurred in March and October, and Bake (1981) found a peak between March and May in *Microtus arvalis*.

We were able to show that, in *Microtus brandti* especially, the autumn hair change is strongly linked to definite times, whereas the time of the spring moults can partly continue until June. Clear differences in moult duration, dependent on simulated photoperiod and temperature changes, were established for *Microtus brandti*. Thus, the coat change to summer fur occurs always more slowly than that to winter fur. This is evident because of the necessity to end the period of higher energy turnover quickly before the onset of winter. Also, the animals need a dense winter coat within a short time if temperatures decrease suddenly; Bake (1981) noted the faster occurrence of the moult in autumn, compared with spring.

Another problem ist the interpretation of all moulting processes within a population throughout the year. Most authors have observed that moulting animals are distributed comparatively evenly throughout the year, but the explanations of this phenomenon are very different. Becker (1952) doubted that there was any seasonal influence. He stated that the start of a single moult cycle was dependent on individual maturation states. As wild rat populations are composed of animals of different ages, he saw no parallel between hair changes and season. The same opinion was expressed by Langenstein-Issel (1950) and Oliviera et al. (1992). However, if we see each individual of a population as passing through the birth-time and age-dependent first and second juvenile moults (see Stubbe and Wiegand 1994) – and this is proven for *Rattus norvegicus* for nearly the whole year – and only then occur seasonal moults, we obtain the appearance of regularly distributed moulting over all months of the year within a population. Thus the reference of Becker (1952) to the birth date distribution over the entire year is the key for the year-long occurrence of moulting.

Stein (1960) considered a type of temporary, indeterminate, but endogenously induced moulting sequence as the original, primary type, but he presumed a secondary parallel between season and moulting cycles. Viro and Koskela (1978) found relationships between the 0 °C-isotherm, the occurrence of compact snow cover, and the development of winter fur in *Micromys minutus*. They reported the completion of the winter pelt for all the animals in a population, one month before attaining the 0 °C-isotherm. Lehmann (1958) observed dependencies of the temporal course of moulting on habitat: he noticed that the hair change of epigean-living animals was more rapid than that of voles and moles, in which it seemed slow and "sluggish".

Rowsemitt et al. (1975) maintained that *Microtus breweri* shows a dependence of moult cycles on reproductive activity. In *Apodemus sylvaticus*, Röben (1969) described a direct seasonal link, but in this species he missed any summer coat, so that the summer-winter rhythm was broken. In our study we have only integrated animals born in March and the first half of April (spring generation) or in the second half of September until first half of November (autumn generation). Only individual mean variations in moult times lead to overlaps by successive moults. In natural populations, animal birth dates may occur from February until October, thus, both different age classes, and numerous moulting states

will be found. Consequently, we can merely state that first and second juvenile moults (often called mature moults) are strongly age dependent, whereas the hair changes of adult animals that follow are more or less subject to season (seasonal moults). We envisage a primarily endogenous rhythm, which can be influenced by environmental factors. STEIN (1954), BÜHLOW (1970) and BAKE (1981) gave similar explanations.

Numerous publications have refered to light regimes as releasers of moulting. Thus, by shortening daylight duration, the development of real winter fur was always observed (BISSONNETTE 1935; BISSONNETTE and BALEY 1944; HARVEY and MACFARLANE 1958; BELJAEV et al. 1964; AL-KHATEEB and JOHNSON 1971; DUBY and TRAVIS 1972; HOFFMANN 1978; LYNCH and GENDLER 1980; ROUGEOT et al. 1984; RHODES 1989). Early studies doubted the influence of temperature; BISSONNETTE and WILSON (1939) reported a minimal influence of temperature changes on moulting processes. HEATH and LYNCH (1983) kept *Peromyscus leucopus* under short-day conditions in both warm and cold environments. Both animal groups grew a winter coat, but the proportion of moulting mice was higher at lower temperaturs. A regulation of moult speed and variation by temperature was found by RUST (1962) in short-tailed weasels. Furthermore, JACKES and WATSON (1975) described a statistical correlation between moult, light duration, temperature, and snow cover by parameter-free correlation coefficients in *Lepus timidus*. In *Mustela vison*, BELJAEV (1976) reported light to be of the greatest importance in the moulting processes. Our investigations on *Microtus brandti* lead us to the conclusion that there is an endogenously fixed rhythm of moult cycles driven by light duration and temperature. This assumption is validated by the fact that animals kept under long-day conditions and at constant temperature (MC 1) develop both a summer and a winter coat. Otherwise, shortening light duration seems to be the releaser of the intermediate winter hair change. This moult is missed under constant light and temperature conditions (MC 1). We believe that temperature and temperature alterations, in particular, have regulatory effects on moult duration. Voles kept under a seasonal temperature regime (MC 3) display a moult duration limited to the minimum time. Moulting in these animals is better adapted to season than is that of animals living without temperature alterations. Animals kept under constant temperature conditions show a higher temporal variability at the start and end of moulting. Also, the results from voles kept in permanent light and at constant temperature (MC 4) support the hypothesis of an endogenous control of the moulting processes. These animals showed the same moult course as animals living under varying environmental conditions.

In our study moulting processes within a single litter seemed to be synchronized; in the natural environment a "priming" effect of some plant compounds, especially in spring, may be possible (SANDERS et al. 1981).

In the case of seasonally dependent aberrations in fur density, two theories exist:

1. The complete replacement of old fur (STEIN 1960, Microtinae)
2. The breakoff of hair points of the winter coat and partial change of woolly into pile hairs (IVANTER et al. 1985, Soricidae).

More is known about the induction of fur density aberrations, therefore we observed the minimum hair density in voles kept under constant light and temperature. Shortening day length leads to increases in fur density, which reaches its highest level if a temperature decrease is added. Significant differences in total hair numbers are noted between constant environmental conditions (MC 1) and a simulated seasonal course of photoperiod and temperature (MC 3).

Furthermore, some authors have found several other factors to influence fur density. HAITLINGER (1968) described a correlation between hair density and body length in *Apodemus*, and SEALANDER (1972) noticed a 78 % increase of hair weight in winter in *Clethrionomys rutilus*. A higher winter fur density was observed by AL-KHATEEB and JOHNSON (1971) in *Microtus agrestis*. Here, the voles were kept under natural and long day

conditions. "Long-day-animals" did not develop a winter coat. The regulation of fur density by day length has also been described in *Sorex araneus* (Borowski 1958), ferrets (Harvey and MacFarlane 1958), *Micromys minutus* (Viro and Koskela 1978), *Microtus arvalis* (Bake 1981), *Phodopus sungorus* (Masuda and Oishi 1988), *Microtus pennsylvanicus* (Rhodes 1989) and various other mammals (Johnson 1984). While these studies attribute a decisive influence to light, our investigations show that temperature also has a regulating function upon fur density.

Acknowledgements

This publication is no. 226 of the "Results of Mongolian-German Biological Expeditions since 1962".
We thank Dr. H. Griffiths from the Departement of Genetics of the University of Leeds for linguistic corrections.

Zusammenfassung

Der Einfluß von Photoperiode und Temperatur auf Fellwechselprozesse bei Microtus brandti (Radde, 1861)

Die Steppenwühlmäuse wurden bei unterschiedlichen Umweltbedingungen (Licht- und Temperaturregime) gehalten und der Haarwechsel an lebenden Tieren über ein Jahr verfolgt. Die Dauer der saisonalen Härungen ist temperaturabhängig, sie verkürzt sich bei schnellem Absinken der Temperaturen deutlich. Saisonale Fellwechsel scheinen endogen fixiert zu sein, da sie auch bei konstanter Temperatur und gleichbleibender Tageslänge auftreten. Allerdings wird die endogene Rhythmik durch variierende Umweltbedingungen verstärkt.

Bei Verkürzung der Tageslänge kann eine intermediäre Härung zwischen zwei Winterfellen ausgelöst werden. Die Haardichte erhöht sich signifikant bei Kurztag und niedrigen Temperaturen.

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Authors' address: Dr. Annegret Stubbe and Dipl.-Biol. Sabine Wiegand, Institut für Zoologie, Martin-Luther-Universität Halle-Wittenberg, Domplatz 4, D-06099 Halle/Saale, FRG

Z. Säugetierkunde 59 (1994) 317–320

ISSN 0044-3468

WISSENSCHAFTLICHE KURZMITTEILUNG

Chromosomes of two rare species of neotropical mammals: Southern pudu (*Pudu puda*) and Bush dog (*Speothos venaticus*)

By A. Schreiber and R. Dmoch

Zoologisches Institut I der Universität Heidelberg and Zoologischer Garten, Frankfurt, FRG

Receipt of Ms. 10. 2. 1994
Acceptance of Ms. 13. 4. 1994

For several years European zoos (Europäisches Erhaltungszuchtprogramm) have coordinated captive breeding projects for two neotropical mammals, the southern pudu (*Pudu puda*) and bush dog (*Speothos venaticus*), including specimens imported from various, mostly unknown geographic origins. Mammalian species are frequently comprised of chromosomally polymorphic or polytypic populations, thus cytogenetic investigations are a useful tool when establishing breeding populations in zoos (e.g. Ryder et al. 1989; Dathe et al. 1989; Schreiber et al. 1993). Since both pudus and bush dogs are fairly delicate mammals to handle for blood sampling, we profited from rare occasions of blood sampling to check whether the initial phase of the captive conservation breeding project had led to a hybridization of unrecognized cytotypes.

The southern pudus kept in European zoos descended from wild captured founders imported in 1966, 1970, and 1972 from unidentified areas of the comparatively small native range of this species. The exact geneology of the four investigated pudus kept at the Cologne Zoo is unknown. Of the six karyotyped bush dogs kept at the Frankfurt Zoo, one male is a first-generation offspring of wild captured parents imported from French Guiana. The other five investigated specimens descended from seven imported animals (with varying percentages of founder representation): They possessed individuals from Paraguay (two wild captured founders) and French Guiana (three wild captured founders) in their ancestry, plus two ancestors acquired from the animal trade without proper information as to their origins. Three-day cultures of peripheral lymphocytes from heparinized blood samples were grown in Chromosomen-Medium B (Seromed, Berlin). After 3–12 hours incubation with colcemide, the preparation of chromosomes was performed as previously described (Schreiber et al. 1993). Per specimen, 10–20 metaphases were photographed and analysed.

The one female and three male karyotyped southern pudus contained a complement of 2n = 70 (NF = 74). The X chromosomes were large metacentrics, whereas all autosomes, with the exception of one pair, were acrocentrics. The largest acrocentric pair of autosomes possessed conspicuous satellite appendages (Fig. 1).

The three female and three male investigated bush dogs showed an identical karyotype of 2n = 74 (NF = 76). Other than the relatively large female sex chromosomes, all autosomes were acrocentrics (Fig. 2). The Y chromosome was a small metacentric.

The karyotype monomorphism found in both sample series does not indicate hybridization of cytotypes during the breeding project. Previous investigations reported karyotypes from one male (Koulischer et al. 1972), and from one male and one female southern pudus to be comprised of 70 chromosomes each (NF = 74) (Spotorno and Fernandez-

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Fig. 1. G-stained karyotype of a male southern pudu (*P. puda*)

Fig. 2. G-stained chromosomes of a female bush dog (*Speothos venaticus*)

DONOSO 1975), findings that are extended to a sample size of seven pudus by the present report. However, cervids, including neotropical species, are notorious for their cytogenetic variability (NEITZEL 1982, 1987). A single northern pudu (*Pudu mephistophiles*) contained 69 chromosomes, including two acrocentrics corresponding to a metacentric, and presumably represented the heterozygote of a translocation polymorphism (NEITZEL 1979). Some authorities include pudus in the genus *Mazama*, the brocket deer (HERSHKOVITZ 1982; CZERNY 1987), whose species display elevated cytogenetic variation, the taxonomic background of which remains to be clarified. In single individual deer classified as *Mazama americana*, the following karyotypes were found: 2n = 68, NF = 74 (TAYLOR et al. 1969; unknown geographic origin of specimen), 2n = 49/50, NF = 72 (JORGE and BENIRSCHKE 1977, *M. americana temana*), 2n = 54 plus two B-chromosomes (NEITZEL 1982, hybrid zoo specimen with parents imported from two regions in Paraguay), and 2n = 52 (NF = 56) plus 4–5 B-chromosomes (NEITZEL 1987, female originating from Paraguay). Interbreeding of the latter cytotype with a male *Mazama gouazoubira* (2n = 70) resulted in presumably infertile offspring with 2n = 61 (plus two B-chromosomes) (NEITZEL 1987). While *M. americana* is so polymorphic, *M. gouazoubira* retains a very conservative karyotype of 2n = 70 (NF = 70), considered to be ancestral for Cervidae (NEITZEL 1982). The bewildering chromosomal variation in the closely related "species" *Mazama americana*, which appears to have evolved within only 2 million years since the presumed colonization of South America (NEITZEL 1987), and the odd-numbered karyotype of the only *Pudu mephistophiles* investigated to date (NEITZEL 1979), suggest that the present sample size of seven karyotyped southern pudus is insufficient to exclude the existence of local chromosomal populations in this species. Pudus are solitary, sedentary deer (HERSHKOVITZ 1982; CZERNY 1987) with probably quite limited interbreeding between regional stocks. Cervids with similar lifestyles, e.g. muntjacs (*Muntiacus*), have fixed so many chromosomal mutations between populations that they represent the ungulates with the most extensive cytological variation (NEITZEL 1982). In Bovidae, dik-diks (*Rhynchotragus*) provide another example of extensive regional chromosomal diversity in a philopatric, territorial ruminant with obviously limited gene flow between stocks (DATHE et al. 1989; RYDER et al. 1989).

Bush dogs are a rare species which avoid human settlements and are not frequently observed (THORNBACK and JENKINS 1982; GINSBERG and MACDONALD 1990). Details of their taxonomy are not well known. CABRERA (1957) recognized three subspecies, *S. v. venaticus, S. v. wingei* and *S. v. panamensis*, which range widely, though sparsely through evergreen rain forests of tropical South America. However, there is no revision of these subspecies, and their exact distributional ranges are unknown. *S. v. venaticus* is believed to inhabit both Guiana and Paraguay, the two countries from where the documented founder animals of the zoo population originated. WURSTER-HILL and CENTERWALL (1982) karyotyped one bush dog of unknown geographic origin and found 2n = 74. Canidae, like deer, include species with microchromosomes or B-chromosomes (e.g. *Nyctereutes, Vulpes*), and in *Nyctereutes procyonides*, the racoon dog, chromosome numbers range from 2n = 42 to 2n = 56/57, the species including chromosomal mosaic individuals, and B-chromosomal polymorphism (WURSTER-HILL et al. 1986). WURSTER-HILL et al. (1988) encountered as many as eight Robertsonian translocation differences between *N. p. procyonides* from China (2n = 54 plus B-chromosomes), and *N. p. viverrinus* from Japan (2n = 38 plus B-chromosomes). YOSIDA and WADA (1985) reported numerous variable chromosomal fissions from the racoon dog population living in Central Honshu, Japan. We have no evidence for B-chromosomes in bush dogs.

Acknowledgements

Colleagues from the Cologne and Frankfurt Zoos supplied us with blood samples. This study was financially supported by a grant by the Cologne Zoo (Prof. Dr. G. Nogge) to promote investigations on species bred within the Europäisches Erhaltungszuchtprogramm.

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Anschriften der Verfasser: Dr. Arnd Schreiber, Zoologisches Institut I der Universität, Im Neuenheimer Feld 230, D-69120 Heidelberg, FRG; Dr. Rüdiger Dmoch, Zoologischer Garten Frankfurt, Alfred-Brehm-Platz 16, D-60316 Frankfurt, FRG

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Z. Säugetierkunde 59 (1994) 5, 257–320

Einem Teil dieser Auflage liegt der Bericht 1993 des Schatzmeisters der DGS bei.

6), 321–384, Dezember 1994 ISSN 0044-3468 C 21274 F

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde

Verlag Paul Parey Hamburg

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

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Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologiezentrum der Christian-Albrechts-Universität, Am Botanischen Garten 9, D-24118 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

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Fortsetzung 3. Umschlagseite

Printed in Germany by Westholsteinische Verlagsdruckerei Boyens & Co., Heide/Holst.

Z. Säugetierkunde 59 (1994) 321–325

ISSN 0044-3468

Neue Nachweise der Schabrackenspitzmaus *(Sorex coronatus)* in Baden-Württemberg durch Polyacrylamidgel-Elektrophorese

Von H. Turni und R. Schönherr

Zoologisches Institut, Abt. Physiologische Ökologie, Universität Tübingen, und Max-Planck-Gruppe für molekulare und zelluläre Biophysik, Jena, Deutschland

Receipt of Ms. 12. 4. 1994
Acceptance of Ms. 23. 6. 1994

Abstract

New records of the Jersey shrew (Sorex coronatus) in Baden-Württemberg by polyacrylamide gel electrophoresis

Ascertained are new records and the eastern distribution of *Sorex coronatus* in Baden-Württemberg. The determination of the species *Sorex araneus/Sorex coronatus* was realized by polyacrylamide gel electrophoresis (PAGE) of total blood proteins. 69 animals from different regions of Baden-Württemberg were identified: 43 *Sorex araneus* and 26 *Sorex coronatus.* First records of *Sorex coronatus* exist now for the region Tauberbischofsheim, Mögglingen, Geislingen, Isny and Wangen/Allgäu. Certainly *Sorex coronatus* is spread to the eastern border of Baden-Württemberg.

Einleitung

Die Existenz zweier morphologisch unterschiedlicher *Sorex araneus*-Typen wies bereits von Lehmann (1955) u. a. für das Rheinland nach, doch erst Meylan (1964) gelang mit seiner karyologischen Untersuchung ein wichtiger Schritt zur Klärung der Artproblematik. Anschließende Untersuchungen ergaben, daß *Sorex araneus* ein instabiler Chromosomenrassen-Komplex ist (bedingt durch Robertsonsche Translokationen), von dem sich – neben der Schabrackenspitzmaus *(Sorex coronatus)* – noch ein weiterer, stabiler Karyotyp, die in Spanien und Portugal vorkommende Art *Sorex granarius,* abgrenzen ließ. Die verwandtschaftlichen Verhältnisse innerhalb der *Sorex araneus*-Gruppe konnten schließlich durch Volobouev und Catzeflis (1989) sowie von Wojcik und Searle (1988) geklärt werden.

Die große Variabilität von *Sorex araneus* und die enge Verwandtschaft zu *Sorex coronatus* lassen eine zuverlässige Trennung beider Arten nach äußeren Merkmalen kaum zu (u. a. Neet 1992). Mehrere Trennmethoden wurden entwickelt, die eine Artdiagnose mit Hilfe von Schädelmerkmalen ermöglichen sollen (u. a. Hausser und Jammot 1974; Mys et al. 1985; Handwerk 1987). Obwohl diese Trennmethoden regional 90–96 % richtig zuordnen, muß berücksichtigt werden, daß einige dieser Schädelmaße geographischen Schwankungen unterliegen. Um jede Restunsicherheit auszuschließen, erfolgt die Artdiagnose durch Karyotypbestimmung oder durch Analyse von Serumproteinen mit Polyacrylamidgel-Elektrophorese (PAGE). In letzterem Falle sind beide Arten an ihren Albuminbanden klar zu unterscheiden (Hausser und Zuber 1983; Brünner 1988).

Die Schabrackenspitzmaus ist ein atlantisches Faunenelement. Sie kommt in Nordspanien, Frankreich, in der Schweiz, den Niederlanden und in Belgien vor. Ihre genaue östliche, vermutlich durch Deutschland verlaufende Verbreitungsgrenze ist noch nicht bekannt. Den Nachweisen im Rheinland folgten – meist auf morphologischen Merkmalen basierend – weitere in Niedersachsen, Westfalen, Thüringen, Osthessen, Saarland, Rheinland-Pfalz, Unterfranken und Baden-Württemberg (Hausser 1990; Herrmann 1991; Meinig 1991; Schelper 1988; Schlegel und Becker 1990).

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Für Baden-Württemberg liegen außer aus Nordbaden (Braun und Kischnick 1987) auch biochemisch (PAGE) ermittelte Nachweise vor. Diese betreffen den Raum Südbaden (Brünner 1988), Nordbaden (Brünner 1990) und Schönbuch/Tübingen (Kulzer et al. 1993), insgesamt also die westlichen und zentralen Landesteile.

Ziel der vorliegenden Untersuchung war, mit Hilfe einer sicheren biochemischen Methode (PAGE) die gegenwärtige Verbreitung der Schabrackenspitzmaus in Baden-Württemberg zu erfassen.

Material und Methoden

Für die vorliegende Untersuchung standen 69 Tiere zur Verfügung. Das für die PAGE benötigte Blut (2 µl) wurde mit heparinisierten Mikropipetten aufgenommen und in ein Eppendorfgefäß ausgeblasen; es ist bei 20 °C ca. 10 Stunden, im Kühlschrank (4–8 °C) ca. eine Woche und im Tiefgefrierschrank (–80 °C) mindestens ein Jahr haltbar. Dieser Umstand macht es möglich, bereits verstorbene Tiere (Katzenbeute, Totfunde), die erst Stunden nach ihrem Tod eingefroren wurden, für die PAGE heranzuziehen.

Mit Hilfe der von Speckkäfern gesäuberten und anschließend vermessenen Schädel wurde eine auf Schädelmerkmalen beruhende, vorläufige Artzuordnung unternommen, um die Blutproben sinnvoll auf dem Elektrophoresegel anordnen zu können.

Die PAGE wurde nach der Methode von Hausser und Zuber (1983) durchgeführt (ausführliche Anleitung bei Brünner 1988). Bei *Sorex araneus* und *Sorex coronatus* ergibt sich am Serumprotein Albumin eine deutliche Trennung infolge der unterschiedlichen Ladungen (wie eine SDS-PAGE ergab, ist das Molekulargewicht beider Albumintypen identisch). Während die Acrylamid-Konzentrationen von Sammelgel, Trenngel sowie die Zusammensetzung des Elektrophoresepuffers im wesentlichen beibehalten wurden, erwies sich eine Verdünnung der Blutproben als sehr vorteilhaft. Wurden die Proben in der von Hausser und Zuber (1983) und Brünner (1988) angegebenen Konzentration verwendet, so erschienen die Banden zu dick. Deshalb wurde für eine optimale Bandendicke folgende Blutprobenkonzentration ermittelt:
Lösung I: 3 µl Blut in 20 µl Saline
Lösung II: 3 µl von Lösung I in: 8 µl Saccharoselösung (40 %) + 50 µl 0,075M Tris/HCl pH 8,9 + Spur Bromphenolblau
Probenauftrag: 15 µl Lösung II

Zwischen den Albuminbanden von Spitzmäusen, die erst wenige Minuten bis Stunden tot waren und von Individuen, die bereits 5 Jahre (!) bei –30 °C eingefroren waren, gab es keine Qualitätsunterschiede.

Ergebnisse und Diskussion

Von den 69 Individuen, deren Fundorte sich auf 33 Meßtischblätter von Baden-Württemberg verteilen, konnten durch PAGE 43 Waldspitzmäuse *(Sorex araneus)* und 26 Schabrakkenspitzmäuse *(Sorex coronatus)* sicher identifiziert werden.

Erstmals konnte die Schabrackenspitzmaus im Allgäu (Wangen, Isny) auf der Ostalb (Geislingen, Mögglingen) und bei Tauberbischofsheim (Heckfeld, Boxberg) nachgewiesen werden. Sie erreicht somit überall die Ostgrenze von Baden-Württemberg. In den Abbildungen 1 und 2 wurden alle bisher durch PAGE ermittelten Nachweise von *Sorex araneus* und *Sorex coronatus* kartographisch dargestellt.

Mit diesen Nachweisen ist auch der Anschluß an die auf morphologischen Merkmalen basierenden Funde in Osthessen (Pieper 1978; Meinig 1991) und Unterfranken (Pieper 1978) gelungen.

Obwohl bisher nur wenige vergleichende Daten zur Ökologie beider Spitzmausarten vorliegen, wird angenommen, daß die Verbreitung von *Sorex coronatus* eng an Landschaften mit atlantischem Charakter (ausgeglichene Temperatur- und Feuchtigkeitsverhältnisse) gebunden ist. Hingegen bevorzugt *Sorex araneus* Gebiete mit kontinentalen Verhältnissen (hohe Bodenfeuchte, starke Temperaturschwankungen). Überall dort, wo „kleinräumige Mischklimate mit atlantischen und kontinentalen Charakteristika" (Meinig 1991) vorherrschen, dürften beide Arten gemeinsam vorkommen. Solche Gebiete erwähnte bereits Brünner (1990) auch für Baden-Württemberg. Ebenso konnten im Schönbuch bei

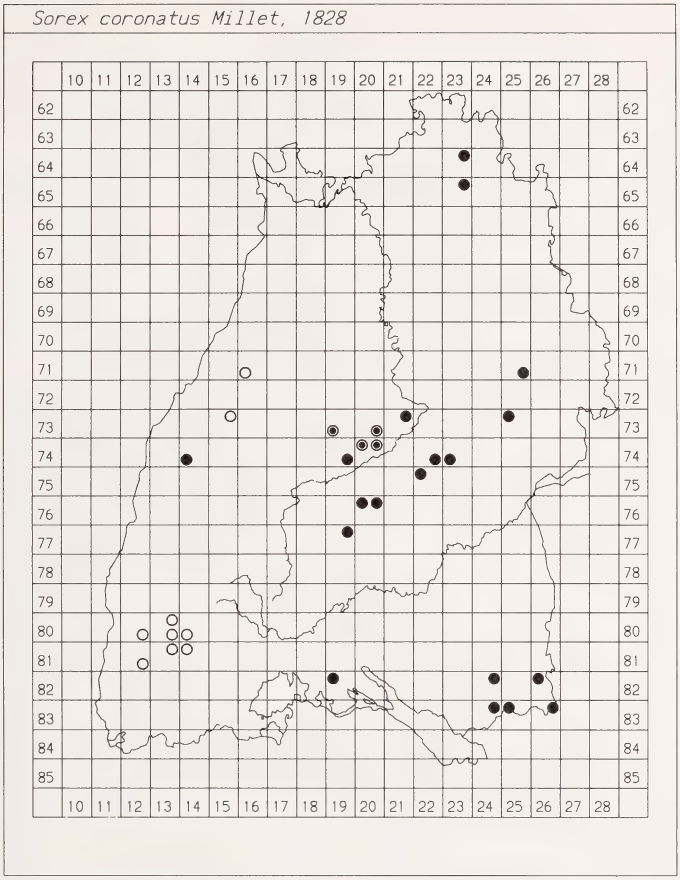

Abb. 1. Erstnachweise von *Sorex coronatus* in Baden-Württemberg durch PAGE. ○ BRÜNNER (1988, 1990); ⊙ KULZER et al. (1993); ● Neue Befunde dieser Studie

Tübingen beide Arten sogar in den gleichen Biotopen gefangen werden (KULZER et al. 1993).

Wie aus den beiden Verbreitungskarten (Abb. 1 und 2) hervorgeht, sind Arealüberschneidungen (oft gleiche Biotope) keine Seltenheit. Eine Auswertung der ökologischen, geographischen und klimatischen Daten aller baden-württembergischen Funde könnte einen interessanten Beitrag zur Ökologie beider Arten liefern. Dies wird im Zusammenhang mit der geplanten flächendeckenden Kartierung in Baden-Württemberg möglich.

Danksagung

Für die finanzielle Unterstützung der Untersuchung im Rahmen des Projektes „Wildlebende Säugetiere in Baden-Württemberg" danken wir dem Ministerium für Umwelt Baden-Württemberg, Stuttgart, und der Landesanstalt für Umweltschutz Baden-Württemberg, Karlsruhe. Für die Hilfe bei der Beschaffung der Spitzmäuse danken wir R. DESCHLE, DR. F. DIETERLEN, E. PALIOCHA, U. SCHARDT und W. SCHLUND. Für die Durchsicht des Manuskriptes danken wir Prof. Dr. E. KULZER. Ganz besonderer Dank gilt Dr. R. FLÖSSER, der diese Untersuchung anregte und förderte. Die Herstellung der Verbreitungskarten erfolgte mit Hilfe eines Programms von N. HIRNEISEN (Öko-Software Tübingen).

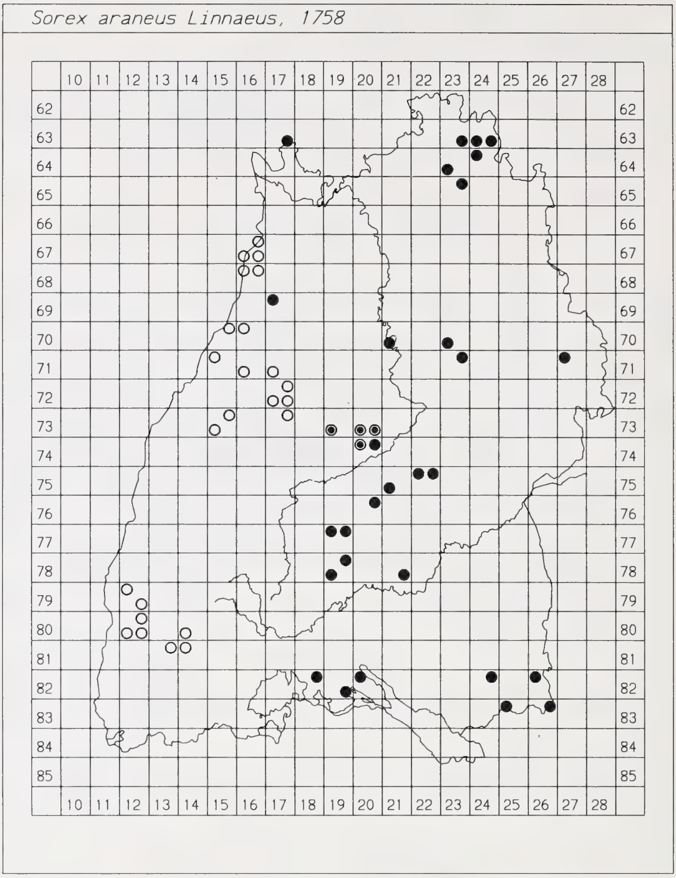

Abb. 2. Identifizierung von *Sorex araneus* in Baden-Württemberg durch PAGE. ○ Brünner (1988, 1990); ⊙ Kulzer et al. (1993); ● Neue Befunde dieser Studie

Zusammenfassung

Das Vorkommen der Schabrackenspitzmaus (*Sorex coronatus* Millet, 1828) in Baden-Württemberg, insbesondere in den östlichen Landesteilen wurde untersucht. Die Trennung der Arten *Sorex araneus* und *Sorex coronatus* erfolgte durch Polyacrylamidgel-Elektrophorese (PAGE) am Gesamtbluteiweiß. Von 69 Spitzmäusen wurden 43 als *Sorex araneus* und 26 als *Sorex coronatus* identifiziert. Erstnachweise von *Sorex coronatus* liegen nun für die Gebiete Tauberbischofsheim, Mögglingen, Geislingen, Isny und Wangen/Allgäu vor. Somit ist die Schabrackenspitzmaus mindestens bis an die Ostgrenze von Baden-Württemberg vorgedrungen.

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Anschriften der Verfasser: Hendrik Turni, Universität Tübingen, Zoologisches Institut, Abt. Physiol. Ökologie, Auf der Morgenstelle 28, D-72076 Tübingen, und Dr. Roland Schönherr, Max-Planck-Gruppe für molekulare und zelluläre Biophysik, Jena, Drackendorfer Str. 1, D-07747 Jena

Z. Säugetierkunde 59 (1994) 326–331

ISSN 0044-3468

Reproductive performance of the Red fox, *Vulpes vulpes*, in Garmisch-Partenkirchen, Germany, 1987–1992

By A. C. Vos

WHO Collaborating Centre for Rabies Surveillance and Research at the Federal Research Centre for Virus Diseases of Animals, Tübingen, Germany

Receipt of Ms. 2. 11. 1993
Acceptance of Ms. 28. 7. 1994

Abstract

The reproductive performance of the red fox *Vulpes vulpes* was studied after the disappearance of rabies between 1987 and 1992 in the county of Garmisch-Partenkirchen. The uteri of 452 adult vixens from the study area, and another 603 vixens from rabies-endemic and rabies-free areas in Bavaria were examined. No significant difference in embryonic litter size was found between 74 rabid and 34 non-rabid vixens in 1987. Furthermore, no difference in mean litter size was found between a rabies-endemic area and the rabies-free study area, Garmisch-Partenkirchen. Litter size and the proportion of barren vixens did not show any significant yearly variation during 1988–1991 in the study area. No difference in litter size (number of placental scars) between the various age classes was found. However, the differences in productivity between the different age-classes were significant, due to a higher proportion of barren yearlings. Although the fox-density increased continually during this field study, apparently the density is still below its carrying capacity. Therefore, no density-dependent effect on the productivity of the red fox population in Garmisch-Partenkirchen could be shown.

Introduction

When a population is reduced below its carrying capacity, an increased productivity may compensate for these losses. MacDonald (1987) described this possibility for the red fox (*Vulpes vulpes*), larger litters being typical for areas with heavy mortality. Could, therefore, a decrease in the productivity be expected in areas where the fox density has increased as a result of the disappearance of rabies? This would be of interest in areas where this important mortality factor of the fox population has disappeared after application of oral vaccination. Data from areas in Switzerland indicate that rabies can kill over 50 % of a local fox population during the height of the epidemic (Wandeler et al. 1974a).

The productivity of a fox population depends on two factors: litter size and the proportion of adult vixens reproducing (Lloyd et al. 1976; MacDonald and Voigt 1985). This study describes the reproductive performance of the fox in the alpine county ("Landkreis") Garmisch-Partenkirchen, Germany. The present European rabies epizootic reached Garmisch-Partenkirchen in the autumn of 1965. For the next twenty years, with the exception of 1970–1971, the county was infected. The rabies-incidence in this area was classified as type four; high oscillations with repeated peaks of rabies-occurrence, often 10 or more cases per 100 km^2 and per year (Jackson and Schneider 1984). Since the application of oral vaccination against rabies in the spring of 1985, no rabid fox has been found here up to the end of this field study in March 1992. The fox density in Garmisch-Partenkirchen increased continually during this study, although it seems that it had not yet reached its carrying-capacity during this period, 1987–1992 (Vos 1993).

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Study area

The study area, the county of Garmisch-Partenkirchen (1012 km^2) in Bavaria is bounded on the south by the Austrian Alps. Approximately 46 % of the county is covered with forest, and 21.5 % is used for agricultural purposes (mainly pastures). The northern part (altitude 600–850 m) of Garmisch-Partenkirchen consists of hilly landscape, covered with a mixture of woods and grassland. The central and southern parts are characterized by mountain-ranges, up to 2964 m, interspersed with valleys and mountainslopes covered with forest. Above tree-line, steep and ragged landscape dominates, with a few scattered alpine meadows.

Material and methods

The data presented here came from a study on fox population dynamics after the disappearance of rabies in Garmisch-Partenkirchen. Uteri were obtained from carcasses of adult vixens (n = 452) killed or found dead in the study area between November 1987 and March 1992. The vixens were collected throughout the year. Litter size was determined from counts of implanted embryos and, after parturition, by placental scar counts, as described by Vos (1993). Since the placental scars persist, they were also used to determine whether or not a vixen had been reproductively active during the last breeding season. The term "barren" includes all adult vixens that failed to reproduce; i. e., those that did not ovulate or failed to implant or lost the entire set of implanted embryos before parturition. To examine the relationship between rabies and the reproductive performance of foxes, vixens (n = 603) from rabies-endemic and rabies-free areas in Bavaria were examined. These vixens consisted of animals delivered for rabies diagnosis collected annually from February to April 1987 through 1991. The age of the vixens was estimated by radiography of canine teeth and/or by counting cementum annuli in the first premolars or canines (Vos 1993).

Results

In spring 1987, in Bavaria, the average number of implanted embryos of rabid vixens ($\bar{x}$ = 5.57, n = 74) did not differ significantly from non-rabid vixens ($\bar{x}$ = 6.26, n = 34) (Kolmogoroff and Smirnoff Test, D = 0.28, n. s.). Also, no significant difference could be observed between the average number of implanted embryos in vixens from a rabies-infected area, the district ("Regierungsbezirk") of Schwaben ($\bar{x}$ = 5.68, n = 29), and those from the rabies-free county of Garmisch-Partenkirchen since 1985 ($\bar{x}$ = 5.75, n = 16) (Student's t-Test, t = 0.16, df = 15). Apparently rabies has no direct influence on litter size. The frequency distribution of the number of placental scars in vixens from Garmisch-Partenkirchen between 1988 and 1991 is presented in table 1. No significant differences in the average number of placental scars (Student's t-Test) and the frequency distribution (Kolmogoroff and Smirnoff Test) could be observed among years.

The average litter size based on the number of embryos was higher than the average litter size based on the number of placental scars in vixens from Garmisch-Partenkirchen. This difference was a result of the period in which the samples were taken. Vixens with implanted embryos were delivered only during early-pregnancy stages; only prenatal losses during implantation and these early pregnancy stages could be considered. How

Table 1. **Number of placental scars in vixens in Garmisch-Partenkirchen, 1987–1991**
($\bar{x}$ – mean number of placental scars, SD – standard deviation)

	Number of placental scars									
Year	1	2	3	4	5	6	7	8	$\bar{x}$	SD
1988	1	1	3	3	8	6	1	1	4.8	1.59
1989	–	1	6	10	6	9	1	–	4.6	1.25
1990	–	1	3	8	11	4	4	–	4.8	1.27
1991	–	–	3	4	11	2	–	–	4.9	1.10
Total	1	3	15	25	36	23	8	1	4.8	1.29

ever, by the evaluation of the placental scars, all visible losses between implantation and birth were taken into account. In early summer, on average 4.6 cubs were observed at the den sites (n = 14). The difference between the number of embryos of early pregnancy stages and the number of cubs observed at the den sites, indicated a loss of around 20 %. Litter size of foxes from different areas is shown in table 2.

The productivity of the fox is not only determined by litter size, also the proportion of reproductively active vixens plays an important role. No differences in the proportion of barren vixens could be observed for Garmisch-Partenkirchen between the years 1988–1991 ($\varkappa^2$-Test, $\varkappa^2 = 4.27$, df = 3, n. s.). The yearly productivity of the vixens (i. e. including barren animals) in Garmisch-Partenkirchen was estimated on the basis of the mean number of placental scars and the proportion of barren vixens (Tab. 3). For productivity, no differences among years could be shown (analysis of variance, F = 0.72, df[3,135], n. s.). 15.3 % of the examined adult vixens (n = 170) were barren. Of these 26 barren vixens, 69.2 % were yearlings, 19.2 % were 2-year olds and two vixens were over four years of age. The proportion of barren yearlings was significantly higher compared to the other age classes ($\varkappa^2$-Test, $\varkappa^2 = 6.5$, df = 1, $P < 0.05$).

In table 4 the mean litter size (placental scar counts) and the proportion of barren vixens are presented for the different age classes. No age-dependent effect on litter size could be shown (analysis of variance, F = 1.79, df[3.98], n. s.). Also no age-dependent litter size (number of embryos) could be found for vixens in the Bavarian sample (analysis of variance, F = 0.65, df[2,83], n. s.). However, the productivity of yearlings in Garmisch-Partenkirchen was significantly lower than of vixens 3-years of age and older (Duncan-Test, $P < 0.05$). The 2-year-old vixens showed the highest mean litter size. As a result of

Table 2. **Litter size of foxes in different study areas**

Study-area		PS		E	YF	Author
rabies-free	CH	5.2		5.2	4.7	Wandeler et al. (1974)
rabies infec.	CH	5.1		5.1		Wandeler et al. (1974)
Oberlausitz	D	6.7		6.3		Ansorge (1990)
Midwest	USA	7.1		6.8	4.1–4.3	Storm et al. (1976)
London	GB	4.8				Harris and Smith (1987)
Bristol	GB	4.7				Harris and Smith (1987)
	D		6.3			Stubbe (1980)
N-Dakota	USA		2.8–5.0			Allen (1984)
	CH		5.4		4.7	Lloyd et al. (1976)
Bavaria	D		6.2			Lloyd et al. (1976)
	NL		6.0			Lloyd et al. (1976)
Wales	GB		5.5			Lloyd et al. (1976)
Wriezen	D				5.3–6.2	Goretzki et al. (1981)
Garmisch-P.	D	4.8		5.8	4.6	Vos (1993)

PS = placental scars; E = Embryos; YF = cubs at den. In some samples data of PS and E are combined.

Table 3. **Yearly productivity of vixens in Garmisch-Partenkirchen, based on the number of placental scars and the proportion of barren vixens**

	1988	1989	1990	1991
Litter size	4.8	4.6	4.8	4.9
Barren vixens (%)	25.0	7.3	19.1	10.0
Productivity	3.6	4.3	3.9	4.4

Table 4. **Productivity of vixens**

Mean number of placental scars (litter size) and the proportion of barren vixens for different age classes in Garmisch-Partenkirchen

Age class (year)	Litter-size	Barren vixens (%)	Productivity
1–2	4.5	24.0	3.4
2–3	5.3	17.9	4.3
3–4	4.7	0.0	4.7
≥4	4.9	6.8	4.6

the relativly high proportion of barren vixens, the productivity of this age class was below that of older vixens.

Discussion

Like Wandeler et al. (1974b), no difference in the mean number of implanted embryos could be observed between a highly infected area and the rabies-free study area, Garmisch-Partenkirchen since 1985. After the disappearance of the important density-dependent mortality factor, rabies, the red fox density increased continually in Garmisch-Partenkirchen (Vos 1993). However, even the growth rate of the population of this generalist, the red fox, is not unlimited. The population threshold (carrying-capacity) of a certain area is a result of density-independent factors, e. g. habitat structure. However, the population numbers are regulated by density-dependent events (Wehner and Gehring 1990).

Negative density-dependent processes limit the growth rate of the fox population. The occurrence of these feedback mechanisms could indicate that the fox population approaches the carrying capacity. These mechanisms do not necessarily mean an increased mortality rate; a decrease in reproduction performance could also influence the growth-rate. In Garmisch-Partenkirchen, no yearly difference was observed in the two important reproduction parameters; litter-size and the proportion of barren vixens. The foxes in this county live in a very stable environment with a high food supply. Apparently the increased fox density after the disappearance of rabies has not reached its carrying capacity. Therefore, no decrease or yearly fluctuations in the reproductive performance were observed during this field study. This is in contrast to several other studies, where the fluctuating numbers of barren vixens can be seen as a density-dependent regulation mechanism in areas with limited or strongly fluctuating food supplies (Englund 1980; MacDonald 1980; Schantz 1981). Englund (1980) found in the northern corniferous belts of Sweden not only large annual variation in the number of barren vixens, but also in the number of cubs per litter. In these areas foxes depend for food almost exclusively on the fluctuating rodent populations. The observed spatial and temporal differences in the reproductive performance of foxes in the different areas are to a large extent a result of variations in the social structure of the fox populations. In some habitats foxes live in social groups comprised of one adult male and several adult vixens (MacDonald 1979; Schantz 1981), whilst elsewhere foxes live in territorial pairs (Storm et al. 1976). Observations of the above-mentioned family groups have been made in areas of high population density and stable food availability (MacDonald 1980), but also in areas where fox populations experience strong food-resource fluctuations (Englund 1980; Schantz 1981). The subordinate vixens of these groups reproduce only in years when there are abundant food resources. At low or intermediate levels of food abundance only the dominate alpha vixen reproduces (MacDonald 1983).

Like Ansorge (1990), litter size did not show an age-dependent effect in this study.

Contrary to these results, ALLEN (1984) found an increase in ovulation rate and embryonic litter size as a function of increasing female age of foxes in North Dakota. However, HARRIS and SMITH (1987) could only observe a decrease in litter size in extremely old vixens in the London area. In accordance with other studies (HARRIS 1979; ENGLUND 1980) most barren vixens in Garmisch-Partenkirchen were yearlings, hence the productivity of this age class was lower than that of older vixens.

Acknowledgements

I am most grateful to all the hunters who assisted with field work and to Dr. GRÖTSCH and his staff (Landesuntersuchungsamt für das Gesundheitswesen in Südbayern) in Oberschleißheim for their support in the laboratory. Financial support was provided by Klocke Verpackungs-Service GmbH, Weingarten-Baden.

Zusammenfassung

Die Reproduktion des Rotfuchses (Vulpes vulpes) im Landkreis Garmisch-Partenkirchen, Deutschland, 1987–1992

Untersucht wurde die Reproduktionsleistung des Rotfuchses *Vulpes vulpes* nach dem Verschwinden der Tollwut zwischen 1987 und 1992 im alpinen Landkreis Garmisch-Partenkirchen. Uteri von 452 adulten Fähen aus dem Untersuchungsgebiet und die von 603 Fähen aus ganz Bayern wurden auf Anwesenheit von plazentalen Narben oder Embryonen untersucht. Keine signifikanten Unterschiede in der durchschnittlichen Zahl der Embryonen zwischen 74 tollwutpositiven und 34 tollwutnegativen Fähen konnten festgestellt werden. Kein signifikanter Unterschied in der durchschnittlichen embryonalen Wurfgröße konnte während dieser Untersuchung zwischen den Fähen aus dem tollwutinfizierten Regierungsbezirk Schwaben und dem seit 1985 tollwutfreien Landkreis Garmisch-Partenkirchen nachgewiesen werden. Keine signifikanten jährlichen Differenzen im Anteil nicht-reproduzierender Fähen und der Wurfgröße wurden während 1988 und 1991 gefunden. Auch unterschied sich die Wurfgröße nicht zwischen den verschiedenen Altersklassen. Die Unterschiede in der Produktivität der Altersklassen als Folge des höheren Anteils nicht-reproduzierender 1jähriger Fähen waren jedoch signifikant. Die Ergebnisse dieser Untersuchung deuten darauf hin, daß die Fuchsdichte im Landkreis Garmisch-Partenkirchen sieben Jahre nach dem Verschwinden der Tollwut anscheinend ihren kritischen Grenzwert noch immer nicht erreicht hat.

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Author's address: Dr. A. C. Vos, Impfstoffwerk Dessau-Tornau GmbH, Postfach 214, D-06855 Roßlau, Germany

Z. Säugetierkunde 59 (1994) 332–341

ISSN 0044-3468

Crabs *Potamonautes perlatus* in the diet of Otter *Aonyx capensis* and Water mongoose *Atilax paludinosus* in a freshwater habitat in South Africa

By M. G. Purves, H. Kruuk, and J. A. J. Nel

Department of Zoology, University of Stellenbosch, Stellenbosch, South Africa

Receipt of Ms. 23. 3. 1994
Acceptance of Ms. 22. 6. 1994

Abstract

Studied the feeding ecology of sympatric Cape clawless otter and water mongoose at the Olifants River, Cape Province. Crab was an important prey in the diet of both species and faecal analysis was used to determine the extent of dietary overlap. Mean crab size taken by water mongoose was larger than that taken by otters. Fish was the second most important prey in the diet of otters, whereas terrestrial prey comprised a major part of the diet of the water mongoose. Different foraging patterns of the predators and habitat selection by crabs of different sizes could explain the observed variation.

Introduction

Over most of their range in southern Africa the two species of otter – Cape clawless *Aonyx capensis* and spotted-necked *Lutra maculicollis* – coexist with the water mongoose *Atilax paludinosus*. They share the same habitat, albeit that the otters are more aquatic and the water mongoose ranges more often away from water; they show temporal overlap in activity; and some prey items are common to two or all three species (Skinner and Smithers 1990). *Atilax paludinosus* is the most widespread, followed by *A. capensis; L. maculicollis* has a more easterly distribution and unlike the others does not utilize marine habitats.

Both otter species have been little studied. Rowe-Rowe (1977a, b) documented their feeding behaviour in captivity and under natural conditions in Natal, while van der Zee (1981, 1982), Arden-Clarke (1986) and Verwoerd (1987) reported on the food, status, population density and spatial organization of *A. capensis* in marine habitats. Baker (1989) compared the feeding habits of *A. paludinosus* in the wild and in captivity and Maddock and Perrin (1993) reported on their role in an assemblage of viverrids.

Freshwater crabs *Potamonautes* spp. (Family Potamonidae) contributed the major portion of the diet of *A. capensis* in Natal (Rowe-Rowe 1977a), in Lake Victoria (Kruuk and Goudswaard 1990) and in various rivers in the SW Cape (unpubl. data). Du Toit (1980), Louw and Nel (1986), Rowe-Rowe (1977a) and Baker (1989) found crab to be important prey of *A. paludinosus* in freshwater habitats, while Whitfield and Blaber (1980), Louw and Nel (1986), and MacDonald and Nel (1986) found crustaceans of importance in the diet of water mongooses in estuarine and in marine habitats.

Crabs constitute the highest macroinvertebrate biomass in some South African rivers (Hill and O'Keeffe 1992), as do crayfish in some rivers in Italy (Gherardi et al. 1989) and high crab densities have also been recorded in trout streams in Zimbabwe (Turnbull-Kemp 1960). Crustaceans can, therefore, either seasonally or year-round provide an important food base for both otters and water mongoose.

This study discusses the utilization of this resource by sympatric *A. capensis* and *A. paludinosus*. It reports on their diet, the use of crabs and seasonal changes in diet in a

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freshwater habitat, and it discusses differences in foraging patterns underlining the observed variation.

Study area

The study was conducted along a 5 km stretch of the Olifants River ca. 8 km downstream from the Bulshoek Dam (31° 58′ S; 18° 45′ E), some 100 m above sea level and ca. 32 km north and downstream of Clanwilliam. Here the river is slow-flowing with marshlands, reeds or grassy verges, oxbows, large basins and with rapids or rocky pools up to 6 m deep. Vegetation on the banks were mainly grasses and sedges e.g. *Paspalum* sp., *Juncus* sp. and *Prionium* sp. *Sesbania punicea* trees formed thickets right up to the river edge in some places.

Average rainfall at the dam site is 265 mm p.a. (1981–1991), while the total rainfall for 1991 was 275 mm (Weather Bureau, in lit.). There is a rise of approximately 2–3 m in the water level at the study site during June and July, when rainfall is at its peak and the sluices of the Bulshoek Dam are opened. The minimum and maximum air temperatures vary from 19–34 °C in January (summer) to 9–19 °C in July (winter).

The fish species in the study area are mostly exotic, e.g. smallmouth bass *Micropterus dolomieu*, or translocated species, e.g. banded tilapia *Tilapia sparrmanii*, while indigenous species (e.g. *Barbus capensis, B. serra* and *Labeo seeberi*), of which most are endemic, are rare. Juvenile fish (2–8 cm in length) were more abundant during the summer, with a rapid decline in numbers from May/June onwards (Swiegers, pers. comm.).

Material and methods

Collection and analysis of scats

Aonyx scats were usually found < 10 m from the water edge, often in exposed areas. Flat rocks were commonly used for collective sprainting, which probably had a communicatory function (Kruuk 1992), as in the European otter. Such latrines were often used repeatedly over several visits to the study area. Individual scats were also scattered around in areas ranging from flat rocks to grassy banks. The mean diameter of the scats collected (when measurable) was 22.2 mm (SD = 3.63, range = 15.3–30.0, n = 50). No otter scats were found in September.

Atilax scats were also deposited at latrines as well as singly on different substrates, but usually in areas with vegetational cover, often > 10 m from the water edge. The mean diameter was 15.8 mm (SD = 2.2, range = 13.0–20.0, n = 23). No water mongoose scats were collected in April.

Both Cape clawless otter *Aonyx capensis* and water mongoose *Atilax paludinosus* scats were collected during February and November (summer), April (autumn), June (winter) and September (spring) 1991, from latrines as well as individual defecation sites. Otter scats were identified and distinguished from water mongoose scats by size, form, smell and the absence of banded hair as found in water mongoose scats. Only relatively fresh (unbleached) and intact scats were collected; those not positively identified were rejected. Scats were placed separately in paper bags and labelled with the species name, date and site of collection.

Air-dried scats were teased apart and all crab eyestalks, intact or broken, extracted. Other diagnostic prey remains, e.g. fish scales and bones were also removed. Fish were identified using scale characteristics and frogs were identified from skeletal remains.

Crabs were identified as *Potamonautes perlatus* (Milne Edwards). A total of 66 crabs of varying sizes (mean carapace width = 31.6 mm, SD = 13.8, range = 8.5–60.1 mm) were trapped or collected by hand in the study area. Both eyestalks of each crab were measured with an occular ruler in a stereo microscope. The length (L) of an eyestalk was taken as the longest axis from anterior to posterior when viewed from the lateral side. There was no consistent difference in the length of the two eyestalks of individual crabs and it was assumed that they were the same length.

The maximum width of the carapace was measured with calipers and correlated with the eyestalk length. There was a clear numerical linear relationship (Fig. 1), for which

$$C = 8.33E - 11.48 \qquad (1)$$

In this C = carapace width (mm) and E = eyestalk length (mm). The correlation was highly significant ($r^2 = 0.99$, $p < 0.001$).

The crabs were also weighed, and regressions of wet weight (dependant variable) and eyestalk length (independent variable) were calculated. A log-linear relationship was found

$$\log W = -0.72 + 0.319E \qquad (2)$$

where W = wet weight (g) and E = eyestalk length (mm); ($r^2 = 0.96$, $p < 0.001$).

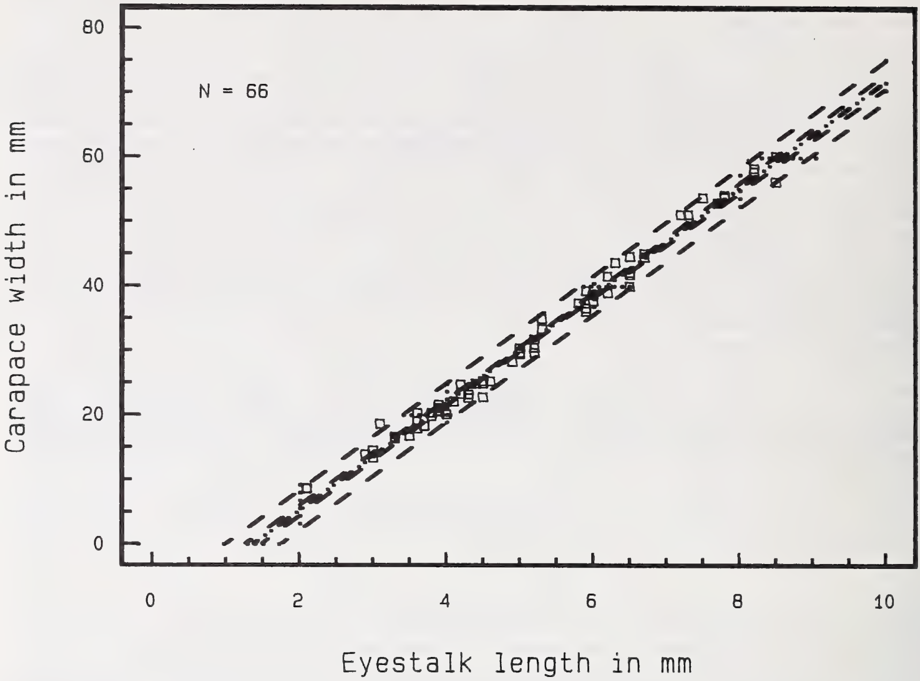

Fig. 1. The relationship between carapace width and eyestalk length in the freshwater crab *Potamonautes perlatus* (r^2 = 0.988, P < 0.001, n = 66, slope = 8.33)

Quantification of data

Prey remains found in scats were expressed as relative percentage of occurrence, calculated by totalling all the occurrences of all the prey items and expressing the actual occurrence of each prey item as a percentage of the total. For each scat dominance of prey type was also found by volumetric analysis of prey items. For that analysis, in a scat consisting mainly of crab remains, crab would be the dominant prey type and the other prey items in this scat would be ignored. The different dominant prey items were than totalled and expressed as a percentage of the total number of scats.

The maximum number of crabs potentially represented by the eyestalks in each scat was taken as the number of eyestalks found, i.e. each eyestalk represented a crab. Half of the number of eyestalks found in each scat was taken as indicating the minimum number of crabs in that scat, implying that a pair of eyestalks represented a crab.

Results

Diet composition

The proportions of prey remains from scat collections at different times of year is shown in figure 2. In both predators, crabs were the most abundant prey at all times, and especially in February. From then until November this proportion in the diet decreases. At all times the diet of *Atilax* was more varied than that of *Aonyx*, with slightly fewer crabs, and also fewer fish, but more terrestrial prey such as rodents and insects. A similar picture emerges from the analyses of scats by estimated bulk of prey remains (Fig. 3).

In total 70 % of the otter scats analysed were dominated by crab and 13.1 % by fish (Tab. 1). *Tilapia sparrmanii* was by far the dominant fish species (85 % occurrence) recorded, with smallmouth bass *Micropterus dolomieu* being the only other fish preyed

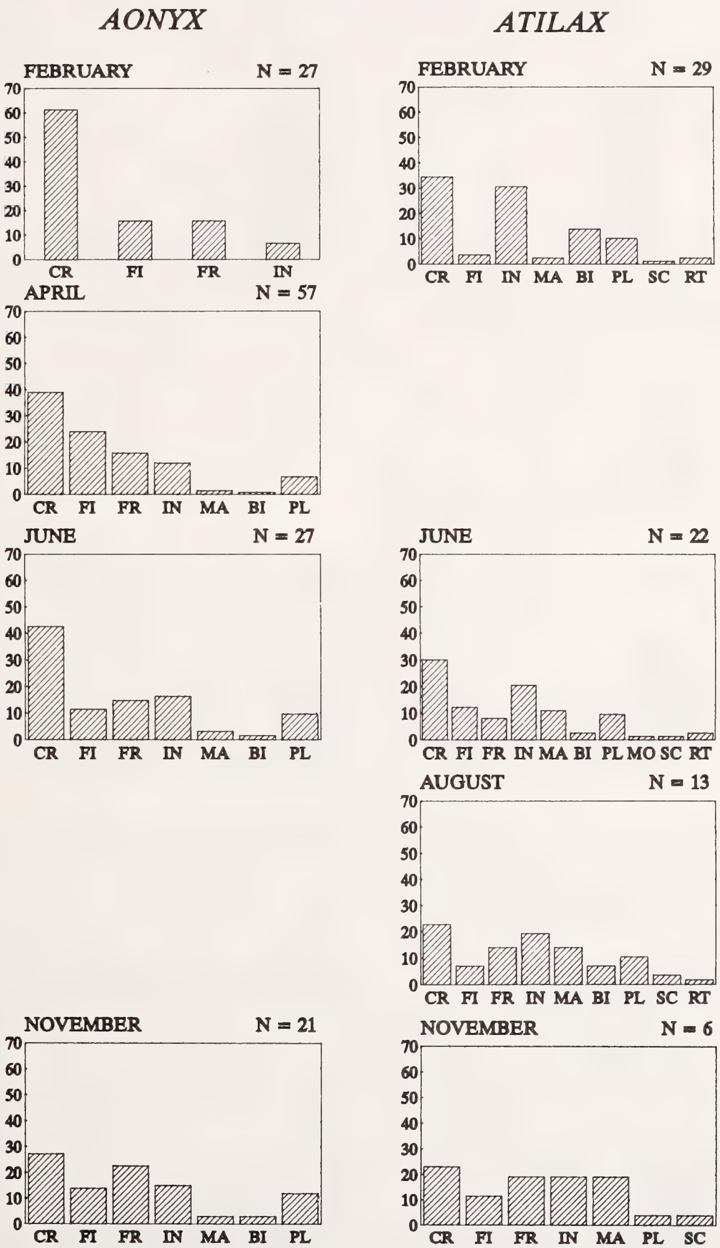

Fig. 2. Relative percentage of occurrence showing seasonal variation of different prey items in the diets of *Aonyx capensis* and *Atilax paludinosus*. (CR = crab, FI = fish, FR = frog, IN = insect, MA = small mammal, BI = bird, PL = plant, MO = mollusc, SC = scorpion, RT = reptile). N = number of scats

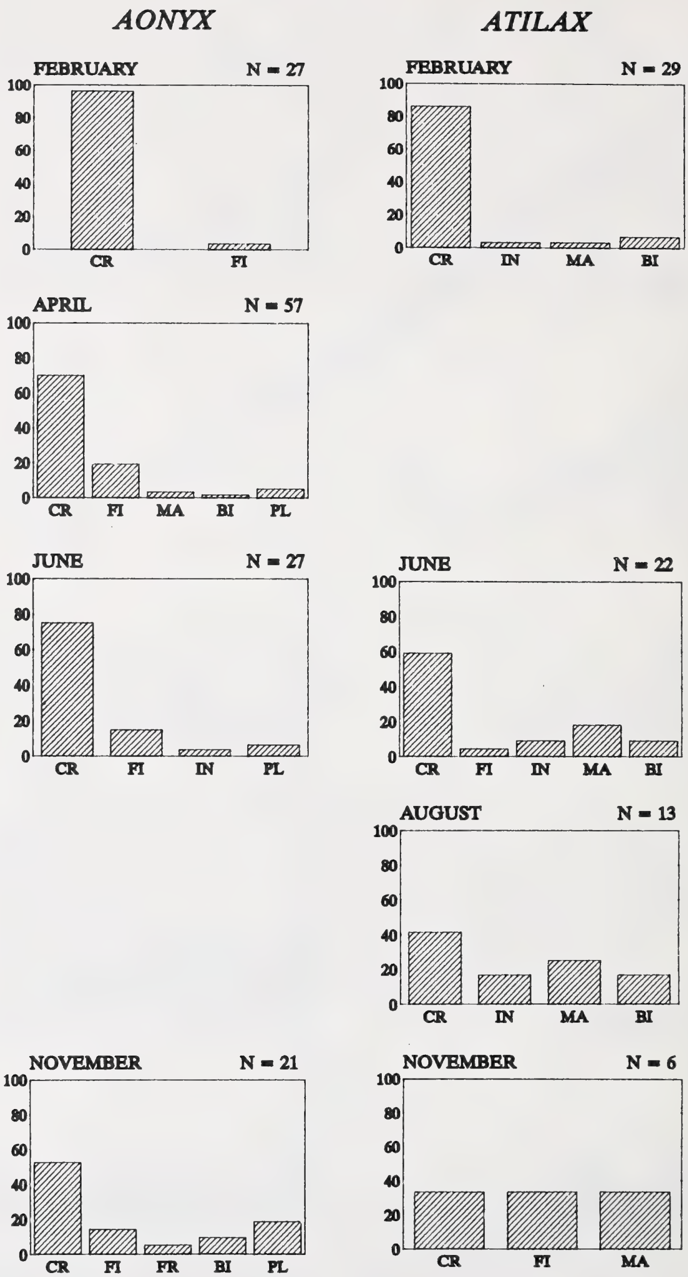

Fig. 3. Percentage dominance of occurrence showing seasonal variation of different prey items in the diets of *Aonyx capensis* and *Atilax paludinosus*. N = number of scats

upon. No remains of indigenous fish species were recorded. The frogs were *Strongylopus grayii* and *Rana fuscigula*. A variety of insect taxa were represented, but only those with a volumetric contribution of > 5 % (suggesting deliberate ingestion) were taken into consideration. These included: Odonata-Aeschnidae nymphs (dragonflies), which were the volumetric dominant insect prey, Coleoptera-Dytiscidae and Scarabaeidae (beetles), Hymenoptera-Formicidae (ants) and Orthoptera-Acrididae (grasshoppers). A small number of spiders (Subclass Arachnida) also occurred. *Otomys saundersiae* was the only small mammal that could be identified from *A. capensis* scats.

Table 1. **Summary of prey items recorded in 132 *Aonyx capensis* scats**

Item	Occurrence	Relative %	% Dominance
Crab	123	40.1	73.5
Fish	57	18.6	14.4
Frog	52	16.9	0.8
Insect	42	13.7	0.8
Plant	23	7.5	6.7
Mammal	6	1.9	1.5
Bird	4	1.3	2.3

Table 2. **Summary of prey items recorded in 70 *Atilax paludinosus* scats**

Item	Occurrence	Relative %	% Dominance
Crab	68	29.0	65.7
Fish	19	8.1	4.3
Frog	19	8.1	0
Insect	55	23.6	7.1
Plant	22	9.3	0
Mammal	23	9.9	14.3
Bird	17	7.2	8.6
Reptile	5	2.1	0
Miscellaneous	6	2.7	0

In 65.7 % of scats of *A. paludinosus* crab was the dominant food (Tab. 2). *Atilax* preyed on a greater variety of insects than *Aonyx*. Coleoptera (beetles) were the most abundant insects found in the diet of *Atilax*. Orthopteran (grasshoppers, locusts and crickets), Lepidopteran (moths and butterflies) and Isopteran (Termites) remains were also identified. Odonata nymphs were less important than in the diet of otters. Mammal prey that could be identified were *O. saundersiae* and *Aethomys namaquensis*.

Size of crabs eaten

Some 1860 eyestalks found in *Aonyx* scats were undamaged enough to be measured. Using equation (1), carapace widths could be calculated (Fig. 4a). The size of crabs varied from a minimum carapace width of 4.3 mm to a maximum of 61.0 mm (mean carapace width = 28.5 mm, SD = 8.88). Of the eyestalks extracted 75 % represented crabs with carapace widths of 15–35 mm (Fig. 4a).

Some scats contained only small crabs; e.g. 27 eyestalks found in one scat all represented crabs with carapace widths < 30 mm. Others consisted of only larger sized crabs, e.g. 6 eyestalks found in one scat represented crabs all with carapace width > 30 mm. Very few (1.7 %) crabs found in the scats had a carapace width > 45 mm.

In the *Atilax* scats analysed 85 eyestalks were found, representing crab sizes ranging from a minimum carapace width of 9.3 mm to a maximum of 47.7 mm (mean carapace width = 29.4 mm, SD = 9.16). Most (62 %) of the crabs had a carapace width of 15–35 mm (Fig. 4b). A significant difference ($p < 0.001$) was found between the sizes of crab preyed upon by otters and water mongoose (Mann-Whitney Test, T = 6494). *Atilax* ate more larger sized crabs, although none of the remains in their diet represented crabs as large as those eaten by *Aonyx*. The distribution of crab-sizes eaten by *Atilax* was bi-modal. The average wet weight of crabs taken was 8.33 g (range: 0.27–74.73 g) for *Aonyx capensis* and 8.98 g (range: 0.75–35.3 g) for *Atilax paludinosus*.

The foraging behaviour of two groups of otters, active at dawn, were observed during February. One group comprised four individuals and the other two. Only crabs were seen to be eaten. The 30 crabs taken were all caught by the otters diving and all were eaten in the

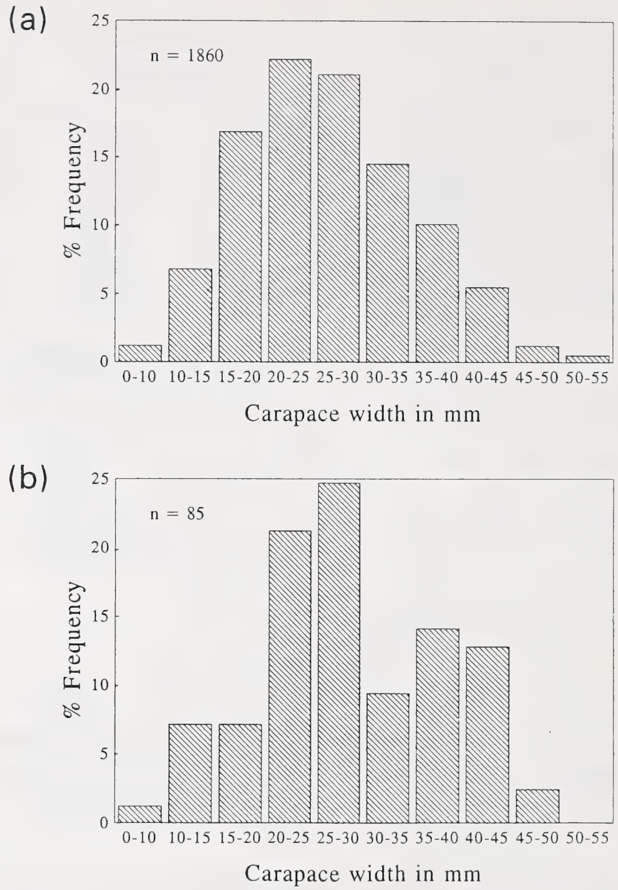

Fig. 4. Frequency of different sizes of crabs, as deducted from the length of eyestalks extracted from the scats of (a) *Aonyx capensis* and (b) *Atilax paludinosus*

water. Larger crabs were eaten with the otter lying on its back and the pincers being fed into the mouth first. Crab catching was concentrated in grassy areas where the depth of the water was <1 m. No observations were made on the foraging behaviour of water mongoose.

Discussion

Although the diets of both *Aonyx* and *Atilax* varied during different seasons, crab remained the single most important prey type for both, and both often ate rather small sized crabs. On average, *Atilax* took larger crabs than *Aonyx*.

Atilax occupies a wider range of habitats than *Aonyx* (Rowe-Rowe 1978; Whitfield and Blaber 1980; Stuart 1981; Skinner and Smithers 1990), it is more mobile on land and wanders greater distances away from water (Rautenbach and Nel 1978). Although there is considerable dietary overlap, terrestrial prey seem to be of more importance in the diet of *Atilax* and the hunting of aquatic prey could be restricted to the shallows (Rautenbach and Nel 1978).

In a marine habitat Louw and Nel (1986) found virtually no dietary overlap between the two species, with *Atilax* concentrating on shore crabs and other terrestrial species, while *Aonyx* took mainly benthic prey. Thus there was a degree of spatial as well as food segregation between the two sympatric species, with *A. paludinosus* foraging along the water edge intertidally and *A. capensis* foraging in the sea itself. Rowe-Rowe (1977a) found a dietary overlap of 65 % between the two species in a freshwater habitat. Both species seem to have much the same activity regimen, being mostly nocturnal and crepuscular (Rowe-Rowe 1978; Maddock and Perrin 1993; own observations).

Predatory and feeding behaviour have been described for the clawless otter (Rowe-Rowe 1977b) and water mongoose (Baker 1989). *Aonyx* swims underwater, turning the head from side to side and often feeling under stones for prey with the fore-feet (Rowe-Rowe 1977b). Rowe-Rowe (1977b) also found that captured crabs were held with both fore-feet and eaten in the water and that the whole crab was eaten. Our observations in the field confirmed this.

Baker (1989) found that *Atilax* sighted crabs when swimming or when walking past water. Their feet were then used in feeling for the crabs, but their heads were not immersed. Once the crabs had been located, however, they ducked their heads under water and caught the crabs in the mouth (Baker 1989). Crabs were taken from the water and eaten on land, and in large specimens parts of the carapace were often discarded (Baker 1989). Empty carapaces, with intact eyestalks, were often seen near the Olifants River and if these were discarded *Atilax* prey, there might be a degree of bias in the sizes of crabs represented in the scats. However some birds e.g. Giant and Pied kingfishers, are also known to prey on crabs and could have been responsible for the empty carapaces.

A difference in size of crab eaten by the two species could be expected, because of the difference in feeding behaviour of the two predators, and differences in movement patterns between small and larger crabs (Hill and O'Keeffe 1992). Smaller crabs were more often found in the grassy verges and muddy banks of the river and in secluded pools away from the main flow. Larger crabs appeared to prefer deeper water. Based on the differences in foraging areas of the otter and mongoose, and therefore availability of different sized crabs, one would expect *Aonyx* to consume larger crabs than *Atilax*. Similarly, the disparity in body size (ca. 3 kg for *Atilax*, 10–12 kg for *Aonyx*) favours *Aonyx* taking larger crabs. However our results do not bear out this prediction.

In Israel Gherardi and Micheli (1989) found larger crabs straying up to 40 m away from the water at night, while the smaller ones hid under rocks and in crevices at this time and did not venture out of the water as often. In the Jonkershoek valley near Stellenbosch large crabs are also occasionally seen venturing far (up to > 500 m) away from the Eerste River. If the same applies to the crabs in the Olifants River, *Atilax* would more readily encounter such crabs as they forage not only along the water edge, but also further afield. This could explain why the average size of crabs found in their diet was larger than that found in the diet of otters.

Atilax utilized a wider range of prey, of which about 45 % was terrestrial. This and the fact that tracks of *Atilax* were often concentrated along the side of the river and at shallows and pools away from the main flow, indicates that they do not forage in water as much as *Aonyx*.

In Thailand the SE Asian small clawed otter *Aonyx cinerea* and the crab eating mongoose *Herpestes urva* occur sympatrically. Both species feed on freshwater crabs *Potamon smithianus*. Here it was found that the mongoose took significantly smaller crabs than the otter (Kruuk et al. 1994 and unpubl. obs.). In contrast to the situation in South Africa the size disparity between these two species is much smaller with *A. cinerea* weighing 5 kg, *H. urva* 3.4 kg. Both are nocturnal and solitary (MacDonald 1984) or occur in small groups (*A. cinerea* – pers. obs.). Ewer (1973) mentions that *H. urva* feeds largely on similar prey as *Atilax paludinosus*, i.e. frogs and Crustacea.

Thus overlap in resource utilization between crab-eating otters and mongooses does not appear to be confined to Africa. However, despite the high proportion of crab in the diet of these various species, there is no evidence to suggest that actual competition occurs. To investigate that important question, further information is required about possible limiting roles of the different prey species in the lives of these carnivores.

Acknowledgements

We thank the Foundation for Research Development and the University of Stellenbosch for providing funds for fieldwork, and travel funds for H. K.; P. R. Swiegers for field assistance; B. Sachse for her help in analyzing scats and assisting in various other ways; H. Huysamen for permission to work on his farm; E. van Dijk for identifying anuran remains; H. Geertsema for identifying insect remains and I. Cordes for translating the German summary.

Zusammenfassung

Krabben, Potamonautes perlatus, in der Nahrung von Kapfingerotter, Aonyx capensis, und Wassermanguste, Atilax paludinosus, in einem Süßwasserhabitat in Südafrika

Die Nahrungsökologie zweier syntoper Arten, Kapfingerotter und Wassermanguste, wurde am Olifants-Fluß in der Kapprovinz, Südafrika, untersucht. Süßwasserkrabben waren ein wichtiger Bestandteil in der Nahrung beider Arten. Anhand von Kotanalysen wurde ermittelt, in welchem Maße sich die Nahrungsspektren überschneiden. Wassermangusten ernähren sich von durchschnittlich größeren Krabben als Otter. Nach Krabben war Fisch der zweitwichtigste Bestandteil der Nahrung der Otter, während terrestrische Tiere einen größeren Teil der Nahrung von Wassermangusten ausmachen. Unterschiede in der Ernährungsweise der beiden Raubtierarten und in der Wahl von Krabben verschiedener Größe können die gefundenen Unterschiede erklären.

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Authors' addresses: M. G. Purves and Prof. J. A. J. Nel, Department of Zoology, University of Stellenbosch, PB X5018, Stellenbosch 7599, R. S. A.; Dr. H. Kruuk, Institute of Terrestrial Ecology, Banchory, Kincardineshire AB31 4BY, Scotland

Z. Säugetierkunde 59 (1994) 342–348

ISSN 0044-3468

Fates of fossorial Water voles, *Arvicola terrestris*, as revealed by radiotelemetry

By F. Saucy

Institute of Zoology, University of Fribourg, Fribourg, Switzerland

Receipt of Ms. 28. 2. 1994
Acceptance of Ms. 18. 7. 1994

Abstract

The fates of 94 fossorial water voles were studied in Switzerland from 1984 to 1986 using radiotelemetry. Fifty-six individuals were recaptured on the study plots at the end of the radiotracking sessions. Taking into account that 34 individuals either died, dispersed or were killed by predators, the fates of 95.7 % of the voles could be assessed, as compared to only 59.6 % if losses were tallied by classical capture-recapture analysis. In most cases, death in situ (10 cases) could be distinguished from the 13 recorded cases of predation (including 4 cases of predation on dispersers). Only 4 tags (4.3 %) were lost. Moreover, the position of the tags and the marks left on the radio-collars allowed the identification of mammalian and avian predators in most cases of predation. Finally, the fates of the 15 dispersers could also be assessed.

Introduction

Dispersal and predation strongly affect population dynamics of small rodents (Lidicker 1985; Krebs 1992; Pearson 1985; Korpimäki 1993). Unfortunately, classical trapping data do not allow the distinction between losses due to mortality and to dispersal. Moreover, mainly because of technical limitations, actual rates of dispersal or of predation are difficult to estimate. Therefore, there is still little data reported from natural populations. However, the recent widespread use of radiotelemetry in small mammal studies allows one to investigate these questions in greater detail (Madison et al. 1985; McShea 1990; McShea and Madison 1992).

The water vole, *Arvicola terrestris*, is a widespread Palaearctic species that presents various ecological forms (review in Reichstein 1982). Contrasting with the lowland populations of *A. terrestris* that are semi-aquatic and live in wet habitats (Wijngaarden 1954; Pelikan and Holisova 1969; Stoddart 1970; Wieland 1973), the fossorial populations (*A. t. scherman*) occur in dry habitats in mountainous parts of Central Europe (Meylan 1981). Fossorial water voles live permanently in underground burrows in grasslands and meadows and they differ from the aquatic populations by many features, including body size, population dynamics, social and mating behaviour (reviews in Reichstein 1982; Saucy 1994a), as well as genetic variability (Saucy et al. 1994). Furthermore, the fossorial populations undergo multiannual fluctuations in density with an unusually long cycle that lasts for 6 years, on average (Saucy 1988a, 1988b, 1994b).

The aim of this study was to investigate the fates of radio-collared fossorial water voles under natural conditions during the course of a multiannual cycle. In this study, data are reported that were collected during experiments conducted in fossorial populations of the water vole in the Jura mountains, as well as the Swiss Alps. In the Jura mountains, the fates of radio-monitored voles were assessed during a decline, a period of low numbers, and the beginning of the increase phase, whereas in the Swiss Alps voles were studied during phases of high density.

Material and methods

Population estimates

Before the beginning of a radiotracking session, population numbers were estimated during two-day live-trapping sessions using the capture-mark-release sampling technique adapted for *A. t. scherman* by AIROLDI (1976, 1978). In all cases, densities (individuals/ha) were computed as the number of captured voles divided by the surface of the plots actually sampled (Tab. 1). Because of the diversity in density conditions (< 1 ind/ha–> 300 ind/ha), varying areas have been sampled during the different experiments. At Les Cluds (near Bullet, Jura Mountains, Switzerland, 1200 m, Tab. 1), where radiotelemetry was applied as a complementary technique during the course of a long-term population study (1982–1986; SAUCY 1988a), population changes were monitored monthly (April–November) on a 0.16 ha quadrat (40 m × 40 m) and three times a year on a larger rectangular 0.5 ha grid (20 m × 200 m) (May, August and October; SAUCY 1988a). Following the decline of the population that occurred in 1984 (the populations became extinct in the above grids), trapping was extended to the remainder of the grassland (15 ha). In the four localities from the Swiss Alps, population densities were estimated on rectangular grids ranging from 0.13 to 0.20 ha.

Table 1. **Study sites, dates, duration of the experiments, density, and phases of the population cycle**

Exp. No.	Location (coordinates)	Dates	Duration of the experiments (days)	Density (ind/ha)	Phase of the cycle
1	Les Cluds (6° 34′ E 46° 51′ N)	7. 6.–25. 10. 1984	35	50	Decline
2	Les Cluds	22. 5.– 5. 7. 1985	56	<1	Low numbers
3	Les Cluds	17. 8.– 4. 9. 1986	19	20	Increase
4	Flendruz (7° 10′ E 46° 30′ N)	15. 8.–21. 8. 1985	7	185	Peak
5	La Comballaz (7° 04′ E 46° 23′ N)	28. 9.–23. 10. 1985	26	311	Peak
6	Le Sépey (7° 03′ E 46° 23′ N)	12. 7.–21. 7. 1986	10	171	Peak
7	Rougemont (7° 14′ E 46° 29′ N)	31. 7.– 6. 8. 1986	7	300	Peak

Radiotelemetry

Following the technique described by several authors (BROOKS and BANKS 1971; BANKS et al. 1975; MADISON 1977; MINEAU and MADISON 1977) 94 voles were equipped with radio-collar transmitters. Ten SM-1 (AVM Instrument Co., Ltd, Livermore, USA) and 10 SS-1 (Biotrack, Wareham, UK) transmitters were used during this study. The tags, weighing 3–4 g and transmitting in the 148–149 MHz frequency band, were powered by 85 mAh batteries that lasted for 35 days, on average. They were shaped with a dental acrylic resin to fit the throat of the voles. Spent batteries were replaced by dissolving the resin in acetone. The radio-collars were fitted around the necks of the animals under ketamine anaesthesia (5 mg/100 g of body weight). The voles were then held in cages overnight to permit recovery from the anaesthesia. Two 3-element Yagi antennae and a LA12-DS (AVM) radio-receiver were used to detect transmitting voles at a range of 50 m to several hundred meters depending on the local conditions. Implant-type transmitters, used by other authors (MIHOK et al. 1988; MADISON et al. 1985), were tested and soon discarded because of an approximately 10-fold reduction in detection range. In order to minimise disturbance, the two Yagi antennae were mounted on tripods and were placed within a range of 20 to 30 m of the voles in such a position that the bearings formed an approximately 90° angle. Localisations of voles were mapped using a reference grid of stakes placed at 2.5 m intervals. Variation in the signal intensity and in the rhythm of transmission enabled determination of whether an animal was active or resting. Voles found to be inactive for more than 5 successive localisations were considered to be dead animals. The radio-collars were then searched out and the causes of deaths were determined. Individuals that left their home-ranges to settle at a distance in new burrows and that were never relocated in their former home-range were classified as dispersers.

Radiotracking sessions

Voles were radiotracked during long-term (up to 8 weeks), as well as short-term (1–4 weeks) sessions (Tab. 1). Long-term sessions involved the few and isolated individuals that could be trapped during the population decline (1984) and the period of low numbers (1985) at Les Cluds (Exp. 1–2; Tab. 1). The animals were monitored once a day or every second day and the sessions were terminated by the death or the disappearance of the animals. During short-term sessions, a selection of 10 to 20 voles, including all those individuals living in a restricted area, were studied simultaneously. These short-term sessions were carried out in the four Alpine localities in 1985 and 1986 and in the Jura mountains in 1986 (Exp. 3–7; Tab. 1). During these experiments, the voles were monitored 3–4 times each day during the 1-week sessions or every second day during the 3- or 4-week experiments.

Finite survival and mortality rates have been estimated for each session. According to Krebs (1989), all rates have been converted into standard time intervals (7 days). The following rates have been considered: 1) Gross survival rates = number alive at the end of a radiotracking session/number of radiocollared individuals released at the beginning of the experiment, 2) Disappearance rate = 1 – gross survival rate. The latter has subsequently been partitioned into death, dispersal and predation rates according to the primary causes of disappearance from the study plots.

Results

At Les Cluds, the population peaked in 1983 (150 ind./ha), declined in 1984 and was nearly extinct in 1985 (Saucy 1988a). No voles could be caught on the 0.5 ha grid in 1985 and extensive additional trapping carried out in the 15 ha neighbouring the grid did not yield more than 7 individuals (0.5 ind/ha; Saucy 1988a). In the Alps, the high densities (> 150 ind/ha) recorded in the four localities suggest that these populations were in a peak phase (Tab. 1).

The fates of the 94 voles that were monitored in all five localities during seven distinct experiments are shown in table 2. Globally, 56 voles (59.6 %) were recaptured alive within the limits of their trapping grid at the end of the experiments, while 10 animals (10.6 %) died in their burrows, 9 individuals (9.6 %) were killed on the study site by a predator and 15 animals (16.0 %) dispersed. The fates of only 4 voles (4.3 %) remained unexplained. These animals disappeared from their burrows and the transmitters could not be located over several square kilometres of surrounding terrain.

Including 4 animals that were killed after having dispersed, 13 cases of predation were recorded during the study (Tab. 2). The level of predation was possibly highest at Les Cluds in 1985 (Exp. 2). Two of the 3 monitored voles were killed by stoats and the fate of the third animal, although unknown, might also be explained by predation (a foraging stoat was observed in the close vicinity of the study plot a few hours before the vole

Table 2. **Fates of the 94 radiotracked voles**

The primary causes of disappearance from the study plots are indicated in columns 4–6, while the fates of the dispersers are given in column 8

Experiment No.	Number of voles radio-tracked	Alive on site	Dead in situ	Killed by a predator	Dispersed	Unknown fate	Killed or disappeared after dispersal
1	14	3	6	1	3	1	2
2	3	0	0	1	2	0	2
3	16	10	0	1	5	0	1
4	11	9	0	0	2	0	0
5	20	12	3	4	0	1	0
6	16	13	0	1	2	0	0
7	14	9	1	1	1	2	0
Totals	94	56	10	9	15	4	5

Table 3. **Finite weekly rates of gross survival and of apparent mortality**

Disappearance rates have been partitioned into 3 components (death, dispersal and predation) according to the primarily identified causes of disappearance (i.e. columns 4–6 of Tab. 2). All rates have been converted into standard 7-day time intervals

Exp. No.	Gross survival rate	Disappearance rate	Death rate	Dispersal rate	Predation rate
1	0.73	0.27	0.15	0.07	0.02
2	0.87	0.13	0.00	0.09	0.04
3	0.84	0.16	0.00	0.13	0.03
4	0.82	0.18	0.00	0.18	0.00
5	0.87	0.13	0.05	0.00	0.06
6	0.86	0.14	0.00	0.09	0.05
7	0.64	0.36	0.07	0.07	0.07
Mean ($\pm$ sd)	0.81 (0.09)	0.19 (0.09)	0.04 (0.06)	0.08 (0.04)	0.04 (0.02)

disappeared). Several cases of predation were also observed at Les Cluds in 1984 and at La Comballaz (sessions 1 and 5) where 3 and 4 of the monitored voles were killed by predators. In the former case, two individuals were caught by predators after having dispersed. Overall, 4 of the 15 dispersers (26.7 %) were killed or disappeared soon after dispersal.

Voles disappeared from the study plots at an average rate of 0.19 per week (Tab. 3; extremes ranging between 0.13 and 0.36). On average, deaths, as well as predation on site contributed to approximately 20 % of weekly losses, while dispersal accounted for approximately twice this amount.

In most cases the predators could be identified owing to the localisation of transmitters and to marks left on the tags. In seven cases, predation was attributed to domestic cats *Felis silvestris* f. *catus*, which, when predating on voles, left many clearly visible biting or chewing marks (little holes) on the collar. The tags were often relocated in barns or houses. Predation by the stoat, *Mustela erminea*, was suspected on several occasions, but could be established beyond doubt in only two cases (at Les Cluds in 1985). In both occurrences, biting marks, similar to those left by cats, were found on the collars. The prey was either devoured in the nest or conveyed over a distance and hidden under a mound of stones. Finally, four cases of predation by avian predators were recorded on the basis of the distinctive marks left by the birds' beaks on the collars. In one case, the transmitter was relocated on a tree. The actual avian predator could be visually identified in three cases. Predation was then attributed to the common buzzard, *Buteo buteo*, in two cases, to the black kite, *Milvus migrans*, in one case, and once to an unknown nocturnal avian predator.

Discussion

It has been frequently reported from vole studies, that a high proportion of animals disappears between successive trapping sessions (reviews in Krebs and Myers 1974; Taitt and Krebs 1985). Few studies, however, have attempted to quantify the relative impact of predation and of dispersal on the vole population dynamics under natural conditions.

Among others, Hilborn and Krebs (1976), using radioactive tags, were mostly unsuccessful in explaining the fates of disappearing meadow voles (*M. pennsylvanicus*) during a population decline, while Mihok et al. (1988) were unable to determine the death causes of radio-tracked individuals. In contrast, McShea (1990), in a pooled analysis of three different studies on *M. pennsylvanicus*, reported estimates of losses to predation

varying between 14 and 41 % of the radiotracked voles. Correspondingly, unexplained losses, however, ranged between 22 % and 36 % (McShea 1990).

Apart from this study, radiotelemetry has been used in previous studies on *Arvicola terrestris* by Leuze (1976) and by Jeppsson (1986, 1990). Both authors, however, studied aquatic populations (in Scotland and Sweden, respectively) and only the former used this method in a demographic perspective. Therefore, the results reported here provide the first estimates of predation and of dispersal in *A. t. scherman* using radiotelemetry.

In this study, I was able to explain the fates of 90 out of the 94 (95.7 %) individuals that were monitored. Moreover, the predator could be identified in 12 of the 13 (92.3 %) instances of ascertained predation. Besides the 19 individuals that died or were killed by a predator in situ, 15 voles dispersed and had left the study plot by the end of the experiment. If these populations had been monitored by trapping, only 56 individuals (59.6 %) would have been recaptured within the study area. Therefore, the fates of 40.4 % of the voles would have remained unexplained instead of only 4.3 % in this study.

Moreover, and in spite of the few numbers involved, these results indicate that dispersal is a risky event in *Arvicola terrestris*, since 4 of the 15 dispersers (26.7 %) were eventually killed by predators. This finding confirms observations made by Leuze (1976) who recorded even higher losses due to predation (mainly from herons) during the dispersal phase of young water voles (up to 50 % of dispersing females).

Several interpretations can be invoked to explain the fates of the voles that disappeared. Transmitter failures can be dismissed, as the voles would have been recaptured in their burrows. It is possible, although unlikely, that the tags suddenly stopped functioning following the death or the dispersal of an animal. Long distance dispersal movements are similarly unlikely. Fossorial water voles usually disperse within 30 to 100 m (Saucy 1988a) and transmitters were searched over large areas, encompassing several hundreds of metres around the study plots. A likely explanation is that the voles were killed by predators that either damaged the transmitters or conveyed them over large distances. Foxes, *Vulpes vulpes*, which were common on the study sites could be, among others, responsible for damaging tags when preying on *A. t. scherman*. The transports of tags over long distances (200–800 m) by various predators (including domestic cats, stoats and avian predators) were recorded on several occasions.

There is a strong trophic relationship between the stoat and the fossorial form of the water vole (Debrot 1981). Stoat populations undergo cyclic fluctuations lagging 1 year behind those of *A. terrestris*. The impact of the stoat on populations of *A. terrestris* is likely to be especially high during declines and periods of low numbers. Although the data are few, this study supports the hypothesis that stoats, which reach their highest densities at the end of the population peaks of *A. t. scherman* (Debrot 1981), might drive already declining populations to extinction. During the course of this study, the few voles that were found to survive the decline at Les Cluds were suspected to have been killed by stoats (Saucy 1988a).

In conclusion, the present study provides preliminary estimates of survival, dispersal and predation rates in *A. t. scherman* using radiotelemetry. It also confirms the potentially strong impact of predators on the population dynamics of this vole. This suggests a role for predation in the unusually long population cycle reported in this species.

Acknowledgements

This study was carried out during the course of a PhD thesis supported by the Station Fédérale de Recherches Agronomiques de Changins, Nyon, Switzerland. I am very grateful to Dr. A. Meylan who supervised the study and to G. Mayor and J.-L. Bertholet for their technical and field assistance. I also would like to thank Drs. J.-P. Airoldi, R. K. Rose and A. Buchala who read and greatly improved earlier drafts of the manuscript. Anonymous referees made helpful comments. The summary was translated into German by M. Krieg.

Zusammenfassung

Erfassung von Einzelschicksalen bei Ostschermäusen (Arvicola terrestris) mit Hilfe der Radiotelemetrie

Mittels Radiotelemetrie wurde in der Schweiz von 1984 bis 1986 das Leben von 94 Ostschermäusen (*Arvicola terrestris scherman*) verfolgt. Am Ende der Radiotelemetrie-Versuche konnten in den Untersuchungsparzellen 56 Individuen wieder gefangen werden. In Anbetracht der Tatsache, daß 34 Individuen entweder starben, auswanderten oder durch Prädation getötet wurden, konnte das Schicksal von 95.7 % der Schermäuse beurteilt werden, im Gegensatz zu 59.6 %, wenn die Verluste mittels der klassischen Fang-Wiederfang-Methode erfaßt worden wären. In den meisten Fällen konnte der Tod in situ (10 Fälle) vom Tod durch Prädation (13 Fälle) unterschieden werden. Nur vier Radiosender (4.3 %) gingen verloren. Darüber hinaus konnten in zwölf von 13 Fällen die Art der Säuger- und Vogelprädatoren bestimmt werden. Zur Identifizierung der Prädatoren wurden die Position der Radiosender und die auf den Halsbändern hinterlassenen Spuren verwendet. Schließlich wurde auch das Schicksal der 15 Auswanderer beurteilt.

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Author's address: Dr. Francis Saucy, Institute of Zoology, University of Fribourg, Pérolles, CH-1700 Fribourg, Switzerland

Z. Säugetierkunde 59 (1994) 349–357

ISSN 0044-3468

Does *Microtus majori* occur in Europe?

By B. Kryštufek, Maria Grazia Filippucci, M. Macholán, J. Zima, M. Vujošević, and S. Simson

Slovene Museum of Natural History, Ljubljana, Slovenia; Dipartimento di Biologia, II Universita di Roma "Tor Vergata", Rome, Italy; Institute of Animal Physiology and Genetics, A.S.C.R., Brno, Czech Republic; Institute for Biological Research, Belgrade, Yugoslavia

Receipt of Ms. 11. 4. 1994
Acceptance of Ms. 9. 6. 1994

Abstract

Voles from Mt. Pelister, Macedonia, which are known from the literature as *Microtus majori*, were subjected to morphometric, karyotypic and electrophoretic analyses, and compared with *Microtus subterraneus* from Slovenia and Montenegro, and *Microtus majori* from Asia Minor. The diploid chromosome number of the Pelister voles (2n = 52) is the same as in *M. subterraneus* from the Balkans. Genetic distances, as revealed by electrophoretic analysis of 27 gene loci between voles from Mt. Pelister and *M. subterraneus* from Slovenia and Montenegro correspond to those generally observed among subspecies of Arvicolidae. Discriminant analysis of 12 raw skull measurements separated successfully *M. majori* from *M. subterraneus.* According to this, the Pelister population should be allocated to the latter, which means that there is no reason to include *M. majori* in the list of the European fauna.

Introduction

Microtus majori Thomas, 1906 is considered to inhabit the Caucasus, northern Turkey and north-western Iran (probably incorrectly given as north-eastern Iran by Gromov and Baranova 1981), but it was recently also reported from the Balkans (Musser and Carleton 1993). Namely, Malec and Storch (1963) and later Felten and Storch (1965) point out the existence of two size classes amongst voles belonging to the *Microtus subterraneus* group from Macedonia. The larger morphotype, from Mt. Pelister, was first ascribed to *Pitymys multiplex* (Fatio, 1905) but later identified as *Pitymys majori* (Felten et al. 1971) or *Microtus majori* (Storch 1982). Subsequent authors reported additional localities for *Microtus majori* in the Balkans: Kivanç (1986) in European Turkey and Niethammer (1986) in northern Greece. However, other recent studies of the rodent fauna of the Balkans have not confirmed the presence of this species in Greek Macedonia (Vohralik and Sofianidou 1987) or failed to mention it within the territory of the former Yugoslavia (Petrov 1992).

The aim of the present study is to reevaluate the identity of the voles from Mt. Pelister which form the basis of the inclusion of *M. majori* in the list of European mammals. This population was compared with *M. majori* from Asia Minor, and with two populations of *M. subterraneus* (de Selys Longchamps, 1936) from south-eastern Europe by biometric, karyotypic and electrophoretic analyses.

Material and methods

We examined 107 voles. Material included voles from museum collections, as well as freshly collected animals. Standard museum specimens are housed in the following collections (acronyms in brackets): British Museum (Natural History), London (BMNH); Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt am Main (SMF); Naturhistorisches Museum Wien, Vienna (NMW); and Slovene Museum of Natural History, Ljubljana (PMS). Material was pooled into four samples: sample

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1: *Microtus majori*, Asia Minor (vicinity of Trabzon, including the type of *majori*; BMNH); sample 2: *M. subterraneus*, Slovenia (PMS); sample 3: Mt. Pelister, Macedonia (NMW, PMS, SMF); sample 4: *M. subterraneus*, Mt. Lovćen, Montenegro (PMS).

All our specimens from sample 2 were collected at Kopanki, Mt. Pelister, or from its vicinity, i.e. in the same area from which voles ascribed to *M. majori* originated.

Chromosomes: Nine individuals were examined karyologically (Pelister 7; Lovćen 2). Standard flame-dried preparations were made directly from the bone marrow of colchicined animal (Ford and Hamerton 1956). In most animals, metaphase spreads were differentially stained by following the slightly modified G-banding and C-banding methods of Seabright (1971) and Sumner (1972). Nucleolar organiser regions (NORs) were revealed by the silver staining technique of Howell and Black (1980).

Allozyme analysis: Tissue samples from 14 fresh specimens (Pelister 6; Lovćen 2; Slovenia 6) were collected and transported in liquid nitrogen to the laboratory, where they were preserved at −80 °C until processed. Homogenates for electrophoresis were obtained from portions of muscle tissue crushed in distilled water. Electrophoretic analysis was carried out on 27 loci, encoding 21 enzymes: α-Glycerophosphatase dehydrogenase (E.C. 1.1.1.8; αGpdh), Sorbitol dehydrogenase (E.C. 1.1.1.4; Sdh), Lactate dehydrogenase (E.C. 1.1.1.27 Ldh-1 and Ldh-2), Malate dehydrogenase (E.C. 1.1.1.37; Mdh-1 and Mdh-2), Malic enzyme (E.C. 1.1.1.40; Me-1 and Me-2), Isocitrate dehydrogenase (E.C. 1.1.1.42; Idh-1), 6-Phosphogluconate dehydrogenase (E.C. 1.1.1.44; 6Pgdh), Glucose-6-phosphate dehydrogenase (E.C. 1.1.1.49; G6pdh), Indophenol oxidase (E.C. 1.15.1.1.; Ipo), Nucleoside phosphorylase (E.C. 2.4.2.1; Np), Glutamateoxaloacetate transaminase (E.C. 2.6.2.1; Got-1 and Got-2), Hexokinase (E.C. 2.7.1.1; Hk), Creatine kinase (E.C. 2.7.3.2; Ck), Adenylate kinase (E.C. 2.7.4.3; Adk), Phosphoglucomutase (E.C. 2.7.5.1; Pgm-1 and Pgm-2), Esterases (E.C. 3.1.1.1; Est-1 and Est-3), Acid phosphatase (E.C. 3.1.3.2; Acph). Adenosine deaminase (E.C. 3.5.4.4; Ada), Aldolase (E.C. 4.1.2.13; Aldo), Mannose phosphate isomerase (E.C. 5.3.1.8; Mpi), Glucose phosphate isomerase (E.C. 5.3.1.9, Gpi).

Electrophoretic procedures follow those described in Filippucci et al. (1988). Isozymes were numbered in order of decreasing mobility from the most anodal. Allozymes were designated numerically according to their mobility relative to the most common allele in the reference population from Mt. Pelister. Allozymic data were analysed as genotype frequencies with the BIOSYS-1 program of Swofford and Selander (1981). The amount of genetic divergence between populations was estimated using the indices of standard genetic identity (I) and distance (D) proposed by Nei (1978). A dendrogram of the genetic relationships between populations was obtained using unweighted pair-group analysis, UPGMA (Sokal and Sneath 1963).

Morphometric analysis: Specimens were preserved as skulls with skins or in alcohol (skulls extracted). Only adult, undamaged skulls (total 53: sample 1: 11; sample 2: 16; sample 3: 24; sample 4: 2) were used for multivariate analysis. Twelve skull measurements were taken from each skull (Fig. 1) using a vernier calliper, accurate to the nearest 0.1 mm. The abbreviations used were: CbL – condylobasal length; RoL – rostrum length; NcL – neurocranial length; DiL – diastema length; MxT – maxillary toothrow length; ZgB – zygomatic breadth; BcB – braincase breadth; IoC – interorbital constriction; BcH – braincase height per bullae; Bc – braincase height without bullae; RoH1 – height of rostrum at the anterior alveoli of the first upper molar; RoH – height of rostrum across the second upper molar.

Variations in metrical characters among samples were analysed by discriminant analyses of raw data using the Statgraphics statistical program (version 5).

Results and discussion

Karyotype

The diploid chromosome number of voles from Pelister (sample 2) is 2n = 52. The karyotype comprises one pair of large subtelocentric and one pair of large submetacentric autosomes. The remaining autosomes are acrocentrics of decreasing size, except for the smallest pair which is metacentric. Distinct short arms can be seen in most of the acrocentric chromosomes. The X chromosome is a large metacentric and the Y is a large acrocentric (Fig. 2).

There are at least four pairs of acrocentric chromosmes possessing NORs. These are located in the telomeric region of one pair of medium-sized chromosomes, and in the pericentromeric area of one small pair. In two pairs of autosomes they are displayed on the apparent short arms (Fig. 3a). The G-banded sex chromosomes are shown in figure 3b. Whereas the X chromosome seems to be of a standard type as far as both size and banding

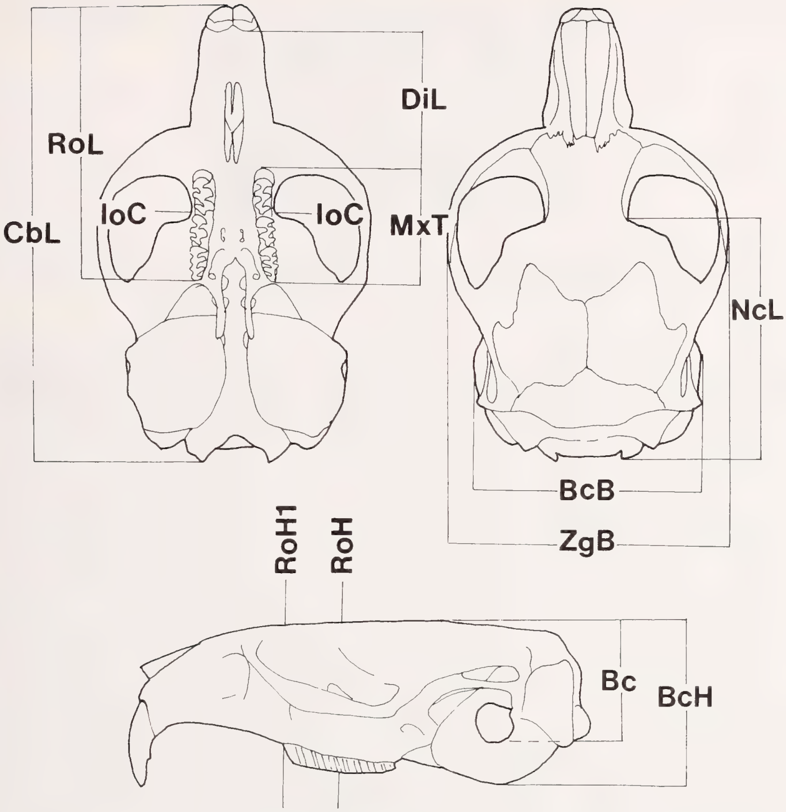

Fig. 1. Cranial measurements of voles used in this study. See text for abbreviations

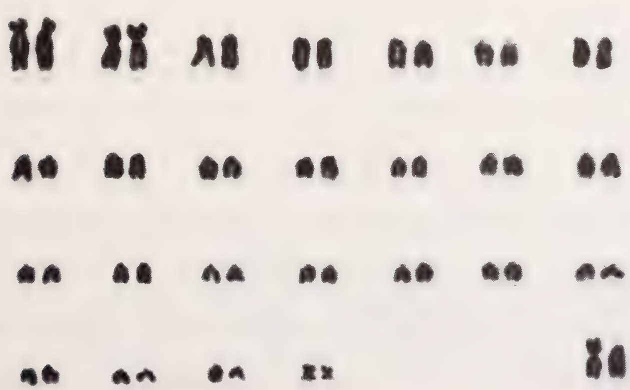

Fig. 2. Conventionally stained karyotype of *Microtus subterraneus* from Mt. Pelister

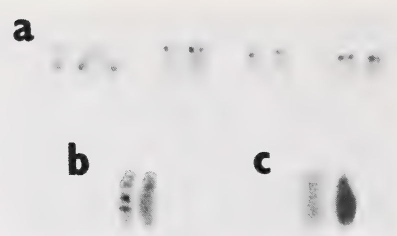

Fig. 3. Chromosomes of *Microtus subterraneus* from Mt. Pelister. a: Four chromosome pairs carrying NORs; b: G-banded; c: C-banded sex chromosomes (the Y on the right)

pattern are concerned, the Y is conspicuously large (nearly as large as the X) and without any obvious G-banding pattern. Only weak C-bands were revealed in some acrocentric autosomes in C-banded metaphases. The X chromosome displays no C-bands. In contrast, the Y chromosome is entirely heterochromatic (Fig. 3c).

The karyotype of the Lovćen specimens appears to be similar to that of the Pelister voles: 2n = 52, with one pair of large subtelocentrics, one pair of large submetacentrics, and one pair of small metacentric chromosomes. Since C-banding was not successful in the only male available from Lovćen, the question of Y chromosome size remains open.

The same diploid number of chromosomes (i.e. 2n = 52) has already been reported for *Microtus subterraneus* from the former Yugoslavia, including populations from Slovenia (Živković et al. 1975), and from Mt. Pelister (Petrov and Živković 1979). *Microtus majori* from the Caucasus displays a different diploid number, 2n = 54 (Zima and Kral 1984), while the karyotype of *M. majori* from its type locality (in the vicinity of Trabzon, northern coast of Asia Minor) has not been studied yet. A karyotype of 2n = 52 chromosomes was also found in *M. subterraneus* from various parts of Europe (see Niethammer 1982; Sablina et al. 1989; Zima and Kral 1984, for review). A large Y chromosome was reported from the Austrian Alps (Gamperl et al. 1982) whereas, in certain other regions of Europe, only the standard, smaller Y has been found (Zima 1984; Sablina et al. 1989). It should be noted, however, that the Y chromosome of the Alpine population is only slightly different from the standard Y chromosome, while the element found in the Pelister population is about twice as large as the standard Y. Thus, this phenomenon cannot be interpreted as being a consequence of a varying degree of chromosome spiralisation in individual preparations, but should be considered to be a specific feature of the study population.

Electrophoretic analysis

Seventeen of the twenty-seven loci analysed were monomorphic and fixed for the same allele in all the populations studied: αGpdh, Sdh, Ldh-1, Ldh-2, Mdh-1, Mdh-2, Me-2, Idh-1, Ipo-1, Np, Got-2, Hk, Ck, Adk, Pgm-2, Aldo, Pgi. The allele frequencies of the polymorphic loci in the populations analysed are given in table 1.

Two loci (Got-1 and Pgm-1) partially discriminated the Mt. Pelister population from *M. subterraneus* from Mt. Lovćen and Slovenia.

From the allele frequencies at the 27 loci tested, Nei's values of genetic identity and distance were calculated amongst populations using all pairwise comparisons (Tab. 2). An UPGMA dendrogram summarizing the genetic relationships between the samples is given in figure 4.

The lowest genetic distance value found was between populations from Slovenia and Mt. Lovćen (D = 0.011). The population from Mt. Pelister displayed higher values of

Table 1. **Allelic frequencies observed at the polymorphic loci analysed in Balkan populations of *M. subterraneus.***

See text for explanation

Locus	Allele	Slovenia	Lovćen	Pelister
Me-1	100	0.83	1.00	1.00
	104	0.17	–	–
6Pgdh	100	0.80	1.00	0.92
	104	0.20	–	0.08
G6pdh	95	–	–	0.08
	100	1.00	1.00	0.92
Got-1	100	0.08	–	1.00
	105	0.92	1.00	–
Pgm-1	100	0.08	–	0.75
	105	0.92	1.00	0.25
Ada	95	–	–	0.33
	100	0.75	0.75	0.67
	105	0.25	0.25	–
Mpi	95	–	–	0.17
	100	0.92	1.00	0.83
	105	0.08	–	–
Acph	100	0.42	1.00	1.00
	105	0.58	–	–
Est-1	95	0.08	–	0.08
	100	0.92	1.00	0.92
Est-3	95	–	–	0.08
	100	0.83	1.00	0.92
	104	0.17	–	–

genetic distance with those from Slovenia (D = 0.067) and Montenegro (D = 0.062). These values correspond to those generally observed among subspecies of Arvicolidae (D = 0.064; Graf 1982) and more generally in other rodents (Filippucci et al. 1991).

Phenetics

Microtus majori possesses three pairs of teats, two inguinal and one pectoral, while the pectoral teats are absent in *M. subterraneus* (Niethammer 1972). All of our seven lactating females from Mt. Pelister had only the two inguinal pairs. In contrast, one standard museum skin from Mt. Pelister (SMF 23,585) clearly shows an additional pectoral pair of teats; this is the only female in the SMF collection which was obviously lactating. The possibility that the number of teats may be polymorphic in the marginal population of *M. subterraneus* is further supported by a personal communication from B. Petrov. Amongst four females that he collected on Mt. Orjen, Montenegro, from which only the *M. subterraneus* karyotype has been reported (Živković et al. 1975), the two lactating females had an additional pair of pectoral teats. A polymorphism in this character has also been reported in *Microtus savii* (de Selys Longchamps, 1838), which has either 2 or 3 pairs of teats (Krapp 1982).

Table 2. **Values of genetic identity (Nei's I, above the diagonal) and distance (Nei's D, below the diagonal), between Balkan samples of *M. subterraneus,* based on 27 loci**

	Slovenia	Lovćen	Pelister
Slovenia	–	0.989	0.935
Lovćen	0.011	–	0.940
Pelister	0.067	0.062	–

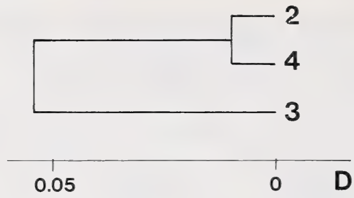

Fig. 4. UPGMA dendrogram summarizing genetic relationships between three populations of *Microtus subterraneus.* D = Nei's (1978) unbiased genetic distance, based on 27 enzyme loci. The cophenetic correlation coefficient is 0.997

The tail appears to be relatively longer in *M. majori* from Asia Minor than in *M. subterraneus* from Slovenia. In the voles from Mt. Pelister the tail is as short as in Slovenian *M. subterraneus* (Fig. 5). However, since external measurements were taken by different collectors, they are likely to have been affected by differences in measuring techniques.

The first two functions resulting from the discriminant analysis of 12 raw skull measurements of four samples (which were responsible for 91.8 % of the variance) clearly distinguished European *M. subterraneus* from Asian *M. majori* (Fig. 6). According to their skull morphology, the Pelister population should thus be allocated to *M. subterraneus.* All specimens of *M. majori* were classified correctly, whilest there was some overlap between samples 2 to 4 (Tab. 3). A total of 9 specimens (= 17 %) was misclassified.

In the next step, samples 2 to 4 (*M. subterraneus*) were pooled and discriminant analysis was repeated. Specimens of both taxa were allocated into their actual groups. Removing five cranial variables (NcL, Dil, NcL, BcH, Mxt) from the discriminant analysis did not affect the classification results. The discriminant function, based on 7 raw skull measurements, could be useful in distinguishing the two species in museum material (Fig. 7):

$$\begin{aligned} DF = & -0.60888 \times CbL - 1.19402 \times ZgB + 3.08761 \times BcB - 3.00499 \times IoC \\ & + 3.18741 \times Bc + 2.79813 \times RoH1 - 3.81314 \times RoH - 25.8104 \end{aligned}$$

The discriminant function has values lower than 1.1 in *M. subterraneus* and higher than 1.5 in *M. majori.*

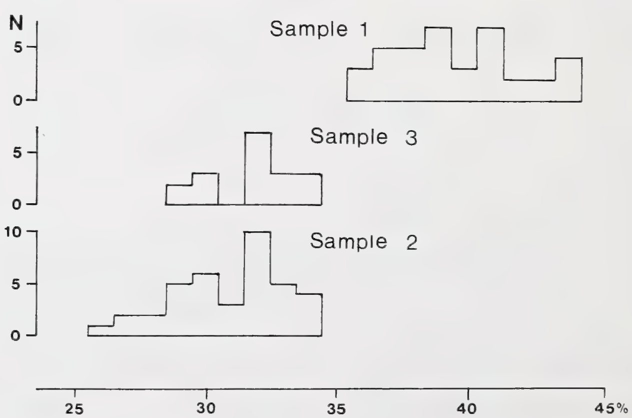

Fig. 5. Frequency histogram of the relative tail length (100× tail / head and body length) in *Microtus subterraneus* (sample 2), *M. majori* (sample 1) and voles from Mt. Pelister (sample 3)

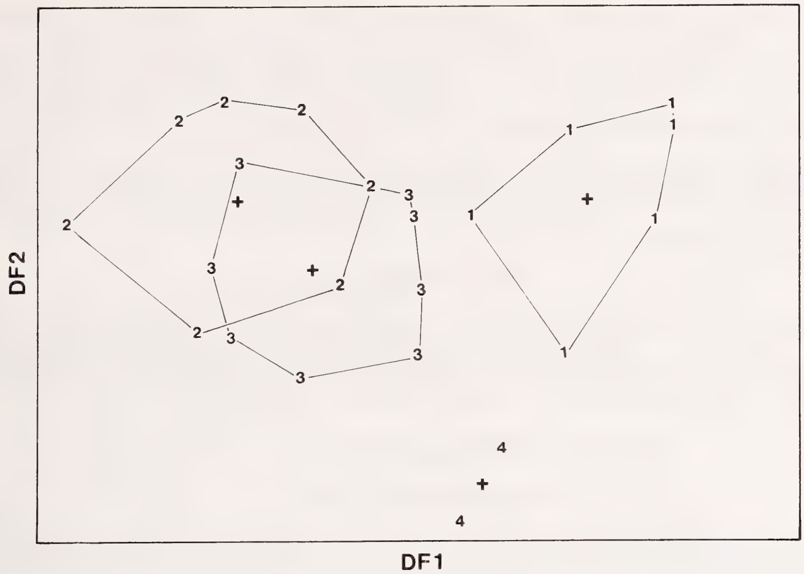

Fig. 6. Projection of four samples of 53 voles on the first two discriminant variates. Polygons enclose scores for all individuals within a locality group, and crosses are placed on group centroids. See text for identifying numbers

Table 3. **Classification table for analysis based on four groups of voles**
Rows are actual and columns are predicted groups (in %)

Actual group	Predicted group 1	2	3	4	Sample size
1 *M. majori*	100.0	0.0	0.0	0.0	11
2 Slovenia	0.0	75.0	25.0	0.0	16
3 Pelister	0.0	16.6	79.2	4.2	24
4 Lovćen	0.0	0.0	0.0	100.0	2

Taxonomic conclusions

The present evidence does not suggest the inclusion of the Pelister voles into Asia Minor's *M. majori.* For the time being, it seems much more appropriate to include them in *M. subterraneus*. This also means that there is no reason to include *M. majori* in the European fauna. Anyhow electrophoretic, as well as karyological data, indicate that the Pelister

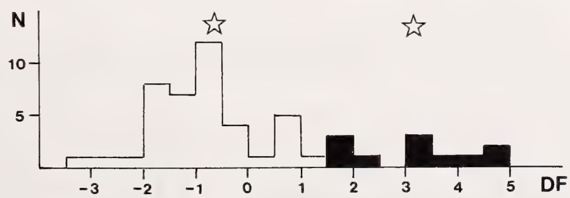

Fig. 7. Distribution of the specimens of *Microtus majori* (black) and *Microtus subterraneus* (white) in the discriminant function axis. Stars represent placement of group centroids

population may be distinct from *M. subterraneus* from the rest of Europe. Its taxonomic relations to other large-sized Balkan voles, usually ascribed to *M. subterraneus* (*hercegovinensis, brauneri*), remain open. According to the electrophoretic analysis, very large voles from Mt. Lovćen, which are even bigger than *M. majori,* are genetically closer to small *M. subterraneus* from Slovenia than to the Pelister voles. The fact that *M. s. hercegovinensis* (Martino, 1940) and other populations of similarly large *M. subterraneus* from Bosnia and Herzegovina have recently been placed into *Microtus multiplex* (Petrov 1992) suggests that the taxonomy of large "*M. subterraneus*" in the Balkans continues to remain a source of debate.

Acknowledgements

We thank the following persons for allowing us to examine specimens under their care: Drs. K. Bauer, P. Jenkins, F. Spitzenberger, and G. Storch. Dr. G. Storch also provided much stimulating discussion and H. Griffiths improved the English text. This research was partly supported by the Ministry of Science and Technology of Slovenia (grant P1-5079-0614 to BK).

Zusammenfassung

Kommt Microtus majori in Europa vor?

Wühlmäuse aus dem Pelister-Gebirge in Makedonien, die in der Literatur als *Microtus majori* geführt werden, wurden morphologischen, karyologischen und elektrophoretischen Untersuchungen unterworfen und mit *M. subterraneus* aus Slowenien und Montenegro sowie *M. majori* aus Kleinasien verglichen. Die diploide Anzahl der Chromosomen (2n = 52) der Wühlmäuse vom Pelister stimmt mit *M. subterraneus* vom Balkan überein. Die genetischen Distanzen, ermittelt durch elektrophoretische Analyse von 27 Genloci, zwischen Wühlmäusen vom Pelister und *M. subterraneus* aus Slowenien und Montenegro entsprechen denen, die gewöhnlich zwischen Subspezies von Arvicolidae festgestellt werden. Mittels einer Diskriminanzanalyse von 12 Schädelmaßen ließ sich *M. majori* und *M. subterraneus* erfolgreich trennen. Danach muß die fragliche Population aus dem Pelister-Gebirge letztgenannter Art zugeordnet werden, was bedeutet, daß *M. majori* aus der Liste der europäischen Fauna zu streichen ist.

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Authors' addresses: BORIS KRYŠTUFEK, Slovene Museum of Natural History, PO Box 290, SLO-61001 Ljubljana, Slovenia; MARIA GRAZIA FILIPPUCCI and SHIMON SIMSON, Dipartimento di Biologia, II Universita di Roma "Tor Vergata", via O. Raimondo, I-00173 Roma, Italy; MILOŠ MACHOLÁN and JAN ZIMA, Institute of Animal Physiology and Genetics, A.S.C.R., Veveří 97, CZ-602 00 Brno, Czech Republic; MLADEN VUJOŠEVIĆ, Department of Genetics, Institute of Biological Research, 29 novembra 142, YU-11060 Beograd, Yugoslavia

Z. Säugetierkunde 59 (1994) 358–365

ISSN 0044-3468

Demographic changes and genetic losses in populations of a subterranean rodent *(Ctenomys maulinus brunneus)* affected by a natural catastrophe

By. M. H. Gallardo and Nélida Köhler

Instituto de Ecología y Evolución, Universidad Austral de Chile, Valdivia, Chile

Receipt of Ms. 21. 1. 1994
Acceptance of Ms. 21. 6. 1994

Abstract

Studied the demographic and genetic effects of a volcanic eruption on two local populations (Río Colorado, Las Raíces) of the fossorial rodent *Ctenomys maulinus brunneus*, in the Andes. Our data represent a unique contribution because the pre-existing demographic data and levels of genetic variation were contrasted with the changes monitored afterwards. Comparative census data of the breeding population size before and after the volcanic eruption, revealed a population decline of about 90 % in Río Colorado. An electrophoretic survey of 23 presumptive enzyme loci detected a considerable reduction of genetic variability in both populations. In Río Colorado, the proportion of polymorphic loci (P) decreased from 47.8 % to 17.4 %, and the expected heterozygosity (H) from 8.9 % to 2.8 %. In Las Raíces, P decreased from 50 % to 0 % and H from 13.2 % to 0 %. Although low genetic variability in fossorial mammals is generally assumed to reflect an adaptation to the stable subterranean niche, in some cases it may be merely the result of genetic drift.

Introduction

Demographic bottlenecks have received significant attention since they have important evolutionary implications for assessing the genetic consequences of reduced population size (Nei and Tajima 1981; Nei et al. 1975; Chakraborty and Nei 1977). These estimates also have implications for conservation projects of mammalian species in fragmented habitats (Lande and Barrowclough 1987; Maruyama and Kimura 1980; Varvio et al. 1986) and for speciation events promoted by founder effects (Barton 1989). Genetic diversity is crucial in an evolutionary sense, and bottlenecks are the quickest means available for loosing genetic variation in natural populations through random fluctuations of population size (Leberg 1992). There is considerable theoretical support for the hypothesis that a natural population passing through a bottleneck should loose genetic variation in direct proportion to the severity of such an event (Chakraborty and Nei 1977; Maruyama and Fuerst 1985a, b; Nei et al. 1975). Despite the theoretical attention and well developed models predicting bottleneck effects (McCommas and Bryant 1990), no actual hints of both demographic and genetic data before and after a bottleneck in the wild have yet been reported. Exemplary studies in mammals (Bonnell and Selander 1974; Harwood and Hall 1990; O'Brien and Everman 1988; O'Brien et al. 1987; Packer et al. 1991) have used reduced genetic variation to infer historical bottlenecks due to the absence of previous suitable parameters. To assess the degree of demographic modifications after a volcanic eruption affecting the fossorial rodent *Ctenomys maulinus brunneus* in southern Chile, we present comparative census data. By comparing electrophoretic data from the same 23 presumptive gene loci before and after the bottleneck, we aim to test the hypothesis that bottlenecks lead to predictable decreases in allozyme variation.

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Material and methods

Field studies were conducted in the austral summer 1986–1987, and 1991–1992, at the type locality of *C. maulinus brunneus* (Río Colorado, Malleco province, Chile, 38° 25′ S, 71° 32′ W; 1,450 m altitude) and in Cordillera Las Raíces, seven km southeast of the topotype locality (Fig. 1). Río Colorado is a flat 4 km^2 high Andean steppe located 3.5 km SW of the Lonquimay volcano. This area sustains a large population of *Ctenomys*, fairly isolated from other local demes by physiographic and vegetational gaps. The Holocenic Lonquimay volcano was dormant until December 1988 when its 50-year period of inactivity was interrupted by a 6-months eruptive phase (Moreno and Gardeweg 1989; Barrientos and Acevedo-Aranguiz 1992).

Pre-eruption estimates of the number of breeding individuals (N) in Río Colorado were obtained from censuses conducted within four grids differing in size, vegetation type, and plant coverage. All animals were removed from the grids, and their reproductive condition was assessed according to Gallardo and Anrique (1991).

Site A: a 50 × 70 m grid on consolidated friable soils which had an 80–90 % cover of bunchgrass interspersed with annual plants. Site B: two grids (40 × 60 m, and 50 × 50 m) on loose volcanic sediments with a 40–50 % cover of annual plants. Site C: a single 60 × 140 m grid on loose volcanic soils which had a 20–25 % cover of annual plants. Field observations confirmed a lack of vegetation from sites B and C owing to the deposition of volcanic ash and scoria following the eruption. There was also a lack of *Ctenomys* activity except in site A where a one hectare grid was sampled in the austral summer 1991.

Pre-eruption estimates of allozymic variation obtained from proteins encoded by 23 loci of 51 pre-eruption specimens from Río Colorado and nine from Las Raíces have been previously reported (Gallardo and Köhler 1992; Gallardo and Palma 1992). The loci assayed were: isocitrate dehydrogenase (ICD-1, ICD-2, Enzyme Commision No. 1.1.1.42), malate dehydrogenase (MDH-1, MDH-2, 1.1.1.37), glutamate-oxaloacetate transaminase (GOT-1, GOT-2, 2.6.1.1), glycerol-3-

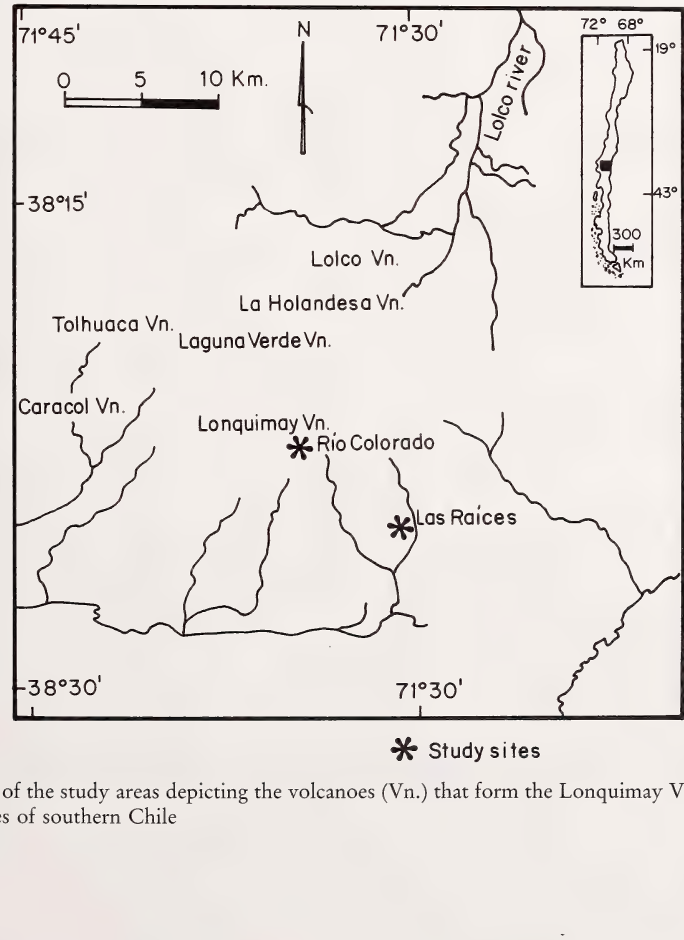

Fig. 1. Map of the study areas depicting the volcanoes (Vn.) that form the Lonquimay Volcanic Front in the Andes of southern Chile

Table 1. **Changes in gene frequencies of polymorphic loci in two populations of *Ctenomys m. brunneus* affected by the eruption of volcano Lonquimay, Chile**

Pre-eruption data for Río Colorado were obtained from Gallardo and Palma (1992), and for Las Raíces, from Gallardo and Köhler (1992)

Locus	Río Colorado		Las Raíces	
	Pre	Post	Pre	Post
Sample size (n)	51	58	9	23
ICD-1				
A	0.020	0.000		
B	0.980	1.000		
MDH-1				
A	0.971	1.000	0.944	1.000
B	0.029	0.000	0.056	0.000
GOT-1				
A	0.010	0.000		
B	0.990	1.000		
GPD				
A	0.961	1.000		
B	0.039	0.000		
Gd				
A			0.000	0.000
B			0.778*	1.000
C			0.222	0.000
GDH				
A			0.000	0.000
B			0.889*	0.000
C			0.111	1.000
LDH-2				
A	0.843*	1.000	0.889*	1.000
B	0.157	0.000	0.111	0.000
XDH-1				
A	0.157	0.034	0.778	1.000
B	0.647*	0.026*	0.000*	0.000
C	0.196	0.940	0.222	0.000
PGM-2				
A	0.814	1.000	0.444	1.000
B	0.186	0.000	0.556	0.000
PGM-3				
A	0.059	0.000	0.000	0.000
B	0.941	1.000	0.944	1.000
C	0.000	0.000	0.056	0.000
PGI				
A	0.951*	1.000	0.000	0.000
B	0.049	0.000	0.944	1.000
C	0.000	0.000	0.056	0.000
PGD				
A	0.078	0.181	0.222	0.000
B	0.902*	0.793*	0.000*	0.000
C	0.020	0.026	0.778	1.000
Mean Polymorphism	47.8 %	17.4 %	50.0 %	0.0 %
Mean N° Allele/locus	1.6	1.3	1.5	1.0
Mean Heterozygosity (direct count)	3.1 %	0.9 %	4.3 %	0.0 %
(Hardy-Weinberg)	8.9 %	2.8 %	13.2 %	0.0 %

* Genotypes for this locus and population deviate significantly from Hardy-Weinberg expectations.

phosphate dehydrogenase (GPD, 1.1.1.8), glucose 6-phosphate dehydrogenase (Gd, 1.1.1.49), glucose dehydrogenase (GDH, 1.1.1.47), lactate dehydrogenase (LDH-1, LDH-2, 1.1.1.27), xanthine dehydrogenase (XDH), phosphoglucomutase (PGM-2, PGM-3, 2.7.5.1.), glucose isomerase (GPI, 5.3.1.9), phosphogluconate dehydrogenase (PGD, 1.1.1.44), albumin (ALB), transferrin (TRFER), hexokinase (HK, 2.7.1.1), acid phosphatase (ACP-1, ACP-2, 3.1.3.2), and malic enzyme (ME, 1.1.1.40). Fifty eight animals from Río Colorado, and 23 from Las Raíces were live-trapped and screened for the same loci after the eruption. Tissue homogenates, buffer systems, migration conditions and mixtures were prepared according to the methods of Selander et al. (1971). Estimates of expected heterozygosity values were compared to the observed numbers and tested for significance by the nonparametric Wilcoxon two-sample test and by a t-test of arcsin transformed genetic data (Archie 1985). All computations of genetic variation were performed with Biosys-1 (Swofford and Selander 1989).

Results

Twenty three animals captured in site A gave an estimate of 66 animals/ha. An additional estimate of 35 animals/ha was generated by pooling density data from the two grids in site B, whereas an estimate of 8.3 animals/ha was obtained from site C. Direct estimates of the breeding population size obtained from census data indicated 1930 animals before the eruption. Based on a density estimate of 20 animals/ha after the eruption in site A, the breeding population size consisted of 168 animals, which corresponds to a 91.3 % reduction in population size after the catastrophe. This estimate provided a rough approximation of the effective population size; at best, it was an upper limit, below which Ne decreases depending on departures from idealized structure (Husband and Barrett 1992).

There was a severe loss of electrophoretic variation in both populations following this bottleneck episode (Tab. 1). Mean polymorphism was significantly reduced; it dropped from 47.8 % to 17.4 % in Río Colorado and reached its minimum value in Las Raíces. Eighty percent of previously polymorphic loci in Río Colorado, and all variable loci in Las Raíces became monomorphic after the bottleneck. As theory predicts, the most frequent allele was more likely to become fixed, but the reverse held for loci GDH and PGM-2 in Las Raíces. Similarly, locus XDH-1, although still polymorphic in Río Colorado, changed significantly in frequency after the eruption (Tab. 1).

The difference between the pre- and post-eruption frequency of heterozygotes was highly significant ($P < 0.0056$; Tab. 2). Further indications for rejecting the null hypothesis of equality between initial and final mean heterozygosities were obtained by congruently significant results of angular-transformed data ($P < 0.004$; not shown). No analogous comparisons were conducted in the Las Raíces sample where the final absence of heterozygotes resulted from a generalized monomorphism.

Table 2. **Observed pre- and post-bottleneck mean heterozygosity values of polymorphic loci in *Ctenomys maulinus brunneus* (Río Colorado)**

The non parametric comparison of mean values is based on the Wilcoxon two-sample test

Locus	Pre-bottleneck Heterozygosity	Post-bottleneck Heterozygosity
ICD-1	0.039	0.000
MDH-1	0.058	0.000
GOT-1	0.020	0.000
GPD	0.076	0.000
LDH-2	0.267	0.000
XDH-1	0.523	0.116
PGM-2	0.306	0.000
PGM-3	0.112	0.000
PGI-1	0.094	0.000
PGD	0.182	0.340
HK	0.179	0.144
ACP-2	0.179	0.051
Total	0.170	0.054
Wilcoxon test: $Z = -2.7651$		$P = 0.0056$

Discussion

Our estimations of density fall within the range reported for other subterranean mammals (Nevo 1979), implying a direct

correlation between number of animals and food supply. Estimates ranging from 3–47 animals/ha in *C. peruanus* (Pearson 1959) to 218 animals/ha in *C. talarum* (Pearson et al. 1968) indicate the large variance of demographic attributes in the genus (Reig et al. 1990).

Theoretically, the major genetic consequence of a bottleneck involves a reduction in the number of alleles, because the variants most at risk are those in low frequency (Chakraborty and Nei 1977). This prediction, supported by our data, reached its maximum expression in the Las Raíces sample. Mean heterozygosity was also affected, especially in Las Raíces where all estimates of genetic diversity reached the most extreme minimum values. Although theory predicts a significant reduction of the number of alleles with less than 10 founders, and even fewer pioneers to affect the average heterozygosity (Chakraborty and Nei 1977; McCommas and Bryant 1990), significant losses in genetic diversity occurred with a larger number of founders, provided a slow population recovery (Lande 1987).

In connection with the genetic effects of demographic bottlenecks, deficiencies in sampling may distort the assessment of heterozygosity levels. Although these estimates appear to be more affected by the number of loci screened than by the number of individuals analyzed (Gorman and Renzi 1979). Considering that the analysis of 8–12 individuals yields, on the average, a heterozygosity estimate within 1% of the value calculated using larger numbers of individuals, sampling biases can be confidently disregarded in our estimations (Gorman and Renzi 1979). Another possible bias stems from the assumption that losses result from the bottleneck itself (Boileau et al. 1992), with no additional genetic cost because a fast demographic recovery is expected. These predictions result in underestimates of the absolute losses, as *Ctenomys* is a k-strategist exhibiting a low instrinsic growth rate (Reig et al. 1990).

Considering the small period of time that has elapsed since the bottleneck, drastic declines in heterozygosity in relation to expected values probably do not result from consanguineous matings, but from a generalized form of inbreeding associated with limited population size (Chesser and Ryman 1986). In this respect, panmictic conditions do not hold since considerable levels of intrademic genetic differentiation strongly suggest population subdivision (Gallardo unpubl. results). Thus, agonistic behaviour and limited dispersal in *Ctenomys* (Gallardo and Anrique 1991) are not consistent with the assumption of a panmixtic unit of 168 individuals, but support an explanation based on the sustained effects of drift acting on disrupted breeding assemblages.

From a conservation viewpoint, bottleneck-flush cycles are major factors contributing to species vulnerability (O'Brien and Everman 1988). Limited population sizes threaten demic persistence when a threshold density value defining mating success is reached (Lande 1987, 1988). Besides, the genetic uniformity attained through repeated bottleneck events also affects demic survival by inbreeding depression (Packer et al. 1991; Wildt et al. 1987), or by a homogeneous inmunological response to environmental disturbances (O'Brien et al. 1985).

Although current interpretations of genic and chromosomal variation patterns in *Ctenomys* emphasize a causal relationship with spatial components (Reig et al. 1990), sustained vulcanism and the tectonically-derived seismic activity in the Andes heighten a component of temporal stochasticity. In this line, previous eruptions of the Lonquimay volcano took place in 1940, 1887 and 1853 (Moreno and Gardeweg 1989). Assuming similar environmental effects, population survivorship, and a one-year generation time (Gallardo and Anrique 1991) the genetic pool of these, and probably other local populations has been altered in generations 135, 101, and 48 before the present.

While contrasting with the multiple karyotypic forms observed in the low land *Ctenomys* species (Gallardo 1991), the karyotypic uniformity reported for species from the Andes (Gallardo 1979) conflicts with the optimal conditions for chromosomal differentiation that stem from limited population size (Lande 1979, 1985; Wright 1941).

Apparently, chromosomal conservatism may be better explained by recurrent vulcanism for when extinctions and recolonizations are frequent, subpopulation divergence is prevented (Maruyama and Kimura 1980) and new colonies are likely to descend from a single ancestral deme (Wright 1941). Considering that the activity of the nearby volcanoes Antuco, Llaima and Villarrica total 36 eruptive events since 1640 (Veblen 1985), the long-term karyotypic uniformity in Andean *Ctenomys* populations appears to be coupled to the structure of the environment. Furthermore, low levels of genetic variability attained by recurrent catastrophes may imitate an adaptive response to the stable subterranean niche (Nevo 1979, 1990) although no selective pressure can counterbalance the effects of drift when populations recover from precarious levels of genetic variability (Maruyama and Fuerst 1985a, b).

Acknowledgements

This research was supported by grant FN 92/0178 and DID UACH grant S-94-29 to MHG.

Zusammenfassung

Demographische Veränderungen und Verluste von genetischer Variabilität bei Populationen des grabenden Nagers (Ctenomys maulinus brunneus) als Folge einer Naturkatastrophe

Es wurden die demographischen und genetischen Auswirkungen eines Vulkanausbruchs auf zwei lokale Populationen (Río Colorado, Las Raíces) des grabenden Nagers *Ctenomys maulinus brunneus* in den Anden untersucht. Ein Vergleich der Populationsgrößen vor und nach dem Vulkanausbruch auf der Grundlage von Zählungsergebnissen in Río Colorado ergab einen Rückgang der Individuenzahlen um etwa 90 %. Die elektrophoretische Untersuchung von 23 Enzymloci zeigte in beiden Beständen eine starke Reduktion der genetischen Variabilität. In Río Colorado sanken die Polymorphierate (P) von 47,8 % auf 17,4 % und der durchschnittliche erwartete Heterozygotiegrad von 8,9 % auf 2,8 %. In Las Raíces sanken P von 50 % auf 0 % und H von 13,2 % auf 0 %. Unsere Daten liefern einen Beitrag zu den wenigen Fällen, in welchen bei natürlichen Populationen Verluste von genetischer Variabilität direkt einem Engpaß in der Populationsgröße zugeordnet werden können. Obwohl die geringe genetische Variation bei grabenden Nagern in der Regel als Anpassung an die stabilen Lebensbedingungen der unterirdischen Nische zugeschrieben wird, kann sie in einigen Fällen lediglich auf genetische Drift zurückzuführen sein.

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Authors' address: Milton H. Gallardo and Nélida Köhler, Instituto de Ecología y Evolución, Universidad Austral de Chile, Casilla 567, Valdivia, Chile

Z. Säugetierkunde 59 (1994) 366–377
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ISSN 0044-3468

Craniometric differentiation and chromosomal speciation of the genus *Proechimys* (Rodentia: Echimyidae)

By M. AGUILERA and M. CORTI

Departamento Estudios Ambientales, Universidad Simon Bolivar, Caracas, Venezuela, and Dipartimento di Biologia Animale e dell'Uomo, Università di Roma 'La Sapienza', Roma, Italy

Receipt of Ms. 11. 3. 1994
Acceptance of Ms. 16. 6. 1994

Abstract

Multivariate morphometrics have been used to investigate the systematics and geographic variation of the spiny rats of the genus *Proechimys* occurring in Venezuela. These populations exhibit extensive differences in their karyotype from 2n = 24 to 2n = 62, and patterns of differentiation in morphological traits of the skull and of the mandible are consistent with a phylogenetic hypothesis suggesting successive events of speciation coupled with increase in diploid numbers. Although no single character by itself can be used to discriminate between taxa, all species and subspecies are clearly distinguishable from each other in a multivariate context.

Introduction

Spiny rats, *Proechimys* (Rodentia: Echimyidae), is a widely distributed genus occurring in the lowland and premontane Neotropical forests of South America, with many extant named species (PATTON 1987; REIG et al. 1980). The entire genus is characterized by a high chromosomal heterogeneity, with diploid numbers ranging from 2n = 14 to 2n = 64 (REIG et al. 1980), and it has been considered as some of the best evidences for genetic change and chromosomal speciation (KING 1993).

An exhaustive review of the genus has been provided by PATTON (1987), who recognized nine groups of species, primarily based upon morphological traits. According to the classification of PATTON (1987) three of these species groups occur in Venezuela, i.e. *trinitatus, canicollis* and *guyannensis*. The range of both *canicollis* and *trinitatus* lies north of the Orinoco river, with only one species of *trinitatus* in the southern part of the basin (*P. hoplomyoides*). The upper Orinoco river groups comprise different species, *P. canicollis* (2n = 24), the only species of the *canicollis* group, and, for the *trinitatus* group, the species *P. trinitatis* (2n = 62), and the nominate superspecies *P. guairae*, with three closely related allospecies: *P. poliopus* (2n = 42), *P. guairae* (2n = 44, 46, 48, 50 and 52) and a third, referred by AGUILERA et al. (1994) as *Proechimys* sp. (2n = 62) (Fig. 1).

The superspecies *P. guairae* represents a remarkable example of a typical rassenkreis, occurring in parapatric contiguous ranges skirting the Maracaibo lake and the mountains of Cordillera de la Costa and Cordillera Andina (Fig. 1). The rassenkreis is characterized by karyomorphs with increasing diploid numbers, from *P. poliopus* (2n = 42) to *Proechimys* sp. (2n = 62), providing evidence that led REIG (1980) to hypothesize a model of chromosomal speciation via centric fissions from lower to higher chromosomal numbers.

The species *P. guairae* is polytypic, and comprises different karyotypic races with diploid numbers corresponding to 2n = 44, 46, 50 and 52 (REIG 1989; AGUILERA et al. 1994). Not all karyomorphs have been assigned a subspecific name, and some are known from the locality from which chromosome preparations were available. Ranges of chromosomal races are apparently contiguous and parapatric, from the lake of Maracaibo to the Unare basin, along the northern coast of Venezuela (Fig. 1). The chromosomal race

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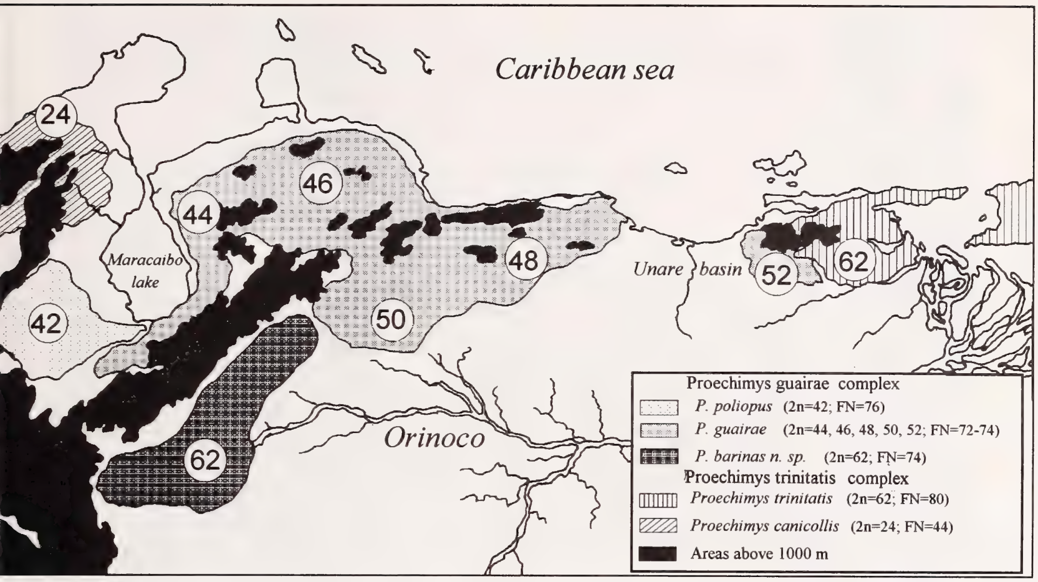

Fig. 1. Map of North Latin America, with the ranges of species and the approximate location of chromosomal races. For the exact location of the localities sampled see Tab. 1

with the highest chromosomal number (2n = 52) occurs in a limited range out of the rassenkreis in the east of Venezuela near *P. trinitatis*. The range is disjunct and separated by the Unare basin (Fig. 1).

There have been some studies on skull morphometrics of spiny rats that focused on some non-geographic aspects of variation, mainly related to growth (Patton and Rogers 1983; Pessoa and Dos Reis 1991a), or on some aspects of intraspecific geographic variation (Dos Reis et al. 1990; Pessoa and Dos Reis 1990, 1991b; Pessoa et al. 1990). However, they refer to other species groups of Patton (1987) such as *P. brevicauda, P. iheringi, P. albispinus, P. dimidiatus, P. guyannensis,* and no analyses are available on the morphometric differentiation of populations and species, namely *casiraguas,* from Venezuela.

The present report describes patterns of morphometric relationships among species and modes of geographic variation in morphometric traits within *casiraguas,* in an attempt to relate these patterns to phylogeny or ecology. Furthermore, we attempt to answer two basic questions: are the karyomorphs morphometrically recognisable with sufficient confidence? Is there any pattern of morphological differentiation that may be interpreted in the light of the established model of chromosomal speciation?

Material and methods

Two-hundred and fifty-five specimens were analyzed representing five species and 12 populations of the genus *Proechimys* in Venezuela (Tab. 1). The species distribution is shown in figure 1 and the exact location of the populations analysed is presented in table 1.

Since the complex displays wide karyotypic variation, most of the animals used in this study were previously karyotyped and correctly assigned to a chromosomal group (Reig et al. 1980; Aguilera et al. 1994) (Tab. 1). Therefore all populations are characterized by their karyotype. Those species and races for which formal description has not yet been carried out will be indicated by us through their diploid number and locality of origin and/or region. These are: *Proechimys* sp. (2n = 62), *P. guairae* "Falcon" (2n = 46), *P. guairae* "Llanos" (2n = 50), and *P. guairae* "Oriente" (2n = 52). *P. poliopus,*

Table 1. **Species and subspecies, locality, diploid number, geographic location (latitude and longitude, acronym and male and female samples)**
Some of the samples were collected from contiguous localities and pooled

Species	Locality	2n	Acronym	Geographic location (latitude and longitude)	Males	Females	Total
P. canicollis	Rio Cachirì	24	*P. can.*	10° 50′ N–72° 13′ W	3	14	17
P. poliopus	Kasmera	42	*P. poli.*	09° 53′ N–72° 43′ W	19	20	39
	Los Angeles del Tucuco			09° 48′ N–72° 50′ W			
P. guairae “Falcon”	La Trilla	46	*P. g.* F	10° 24′ N–67° 45′ W	12	9	21
P. g. guairae	El Limon	48	*P. g. g.* 1	10° 19′ N–67° 38′ W	20	3	23
P. g. guairae	Turiamo	48	*P. g. g.* 2	10° 27′ N–67° 50′ W	12	12	24
P. guairae “Llanos”	Palmero	50	*P. g.* L. 1	09° 44′ N–68° 34′ W	6	6	12
P. guairae “Llanos”	Turén	50	*P. g.* L. 2	09° 16′ N–69° 04′ W	7	7	14
P. guairae “Oriente”	Cueva de Agua	52	*P. g.* O.	10° 10′ N–64° 35′ W	8	10	18
	San Juan de Areo			09° 52′ N–63° 53′ W			
Proechimys sp. (2n = 62)	Guaquitas	62	*P. b.* 1	07° 27′ N–71° 20′ W	12	9	21
Proechimys sp. (2n = 62)	Tierra Buena	62	*P. b.* 2	09° 15′ N–69° 39′ W	14	11	25
	Las Matas			09° 11′ N–69° 35′ W			
Proechimys sp. (2n = 62)	La Nulita	62	*P. b.* 3	07° 19′ N–71° 55′ W	7	9	16
P. trinitatis	Cueva del Guacharo	62	*P. trin.*	10° 10′ N–63° 33′ W	13	12	25

P. guairae “Oriente” and *Proechimys* sp. (2n = 62) Tierra Buena – Las Matas are each represented by two populations (Tab. 1) and have been pooled to increase sample size.

Nineteen distance characters were recorded on the skull and four distance characters on the mandible with the aid of a digimatic caliper (Mitutoyo, 0.01 mm precision). The distance characters are as follows (Fig. 2): Total length (TL): from anterior point of nasal to the sagittal bulge of the occipital; Nasal length (NL): from the anterior point of the nasal to suture with frontal; Basilar length (BL): from the posterior point of the incisor at its alveolus to the anterior border of foramen magnum; Palatal length (PL): from the posterior point of the incisive foramen to the posterior border of the palate; Palatine length (PLL): from the posterior point of incisor at its alveolus to the posterior border of the palate; Upper diastema length (UDL): from the posterior point of the incisor at its alveolus to the anterior point of alveolus M^1; Incisive foramen length (IFL); Alveolar length (UAL): of the upper molar series; Incisor-zygomatic length (IZL): form the posterior point of the alveolus of the incisor to the posterior border of the zygomatic arch; Bulla tympanica length (BTL): longest length of the bulla taken along the axis oblique to the skull length; Fronto-maxillar suture width (FMW); Bizygomatic width (BZW): taken in the widest section; Minimum interorbital width (MLOW): taken over the frontal; Palatal width (PAW): taken in the middle part of the two M^2; Incisive foramen width (IFW): maximum width; Bulla tympanica width (BTW): longest width of the bulla taken along the axis oblique to the skull length; Cranial width (CW): the maximum width taken immediately on top of the external auditory meatus; Maximum height of rostrum (MXHR); Cranial height (CH).

Characters TL, NL, BL, PL, PLL, UDL, IFL, UAL, IZL, BTL, FMW, BZW, MLOW, CW, MXHR, CH correspond to those similarly recorded by Patton and Rogers (1983).

The following four distance characters were recorded on the

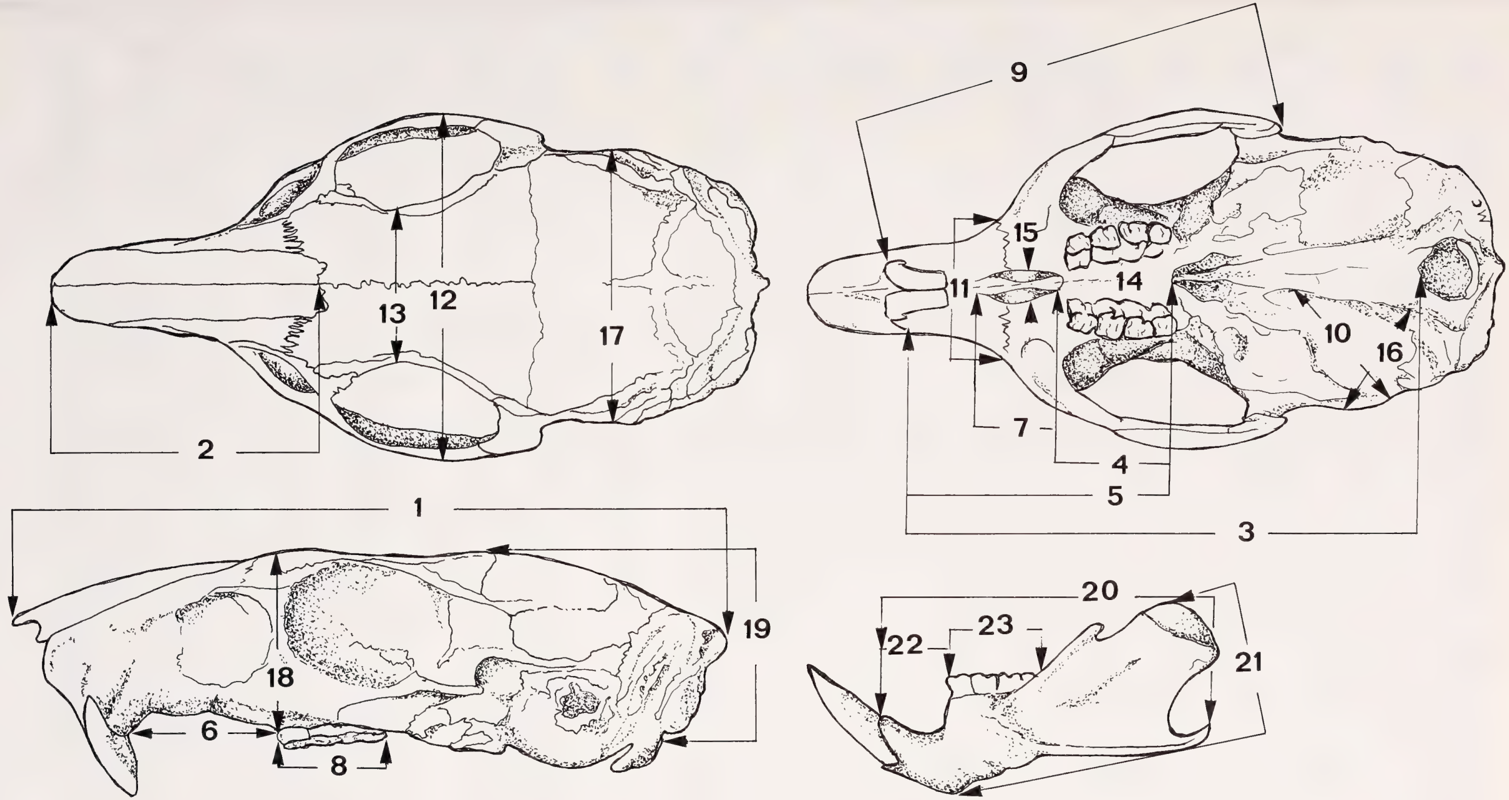

Fig. 2. Characters measured on the skull and the mandible. 1 – Total length (TL); 2 – Nasal length (NL); 3 – Basilar length (BL); 4 – Palatal length (PL); 5 – Palatine length (PLL); 6 – Upper diastema length (UDL); 7 – Incisive foramen length (IFL); 8 – Upper alveolar length (UAL); 9 – Incisor-zygomatic length (IZL); 10 – Bulla tympanica length (BTL); 11 – Fronto-maxillar suture width (FMW); 12 – Bizygomatic width (BZW); 13 – Minimum inter-orbital width (MLOW); 14 – Palatal width (PAW); 15 – Incisive foramen width (IFW); 16 – Bulla tympanica width (BTW); 17 – Cranial width (CW); 18 – Maximum height of rostrum (MXHR); 19 – Cranial height (CH); 20 – Mandibular length (ML); 21 – Mandibular height (MH); 22 – Inferior diastema length (IDL); 23 – Inferior alveolar length of the lower molars (IAL)

mandible: Mandibular length (ML): from the posterior point of the incisor at its alveolus to the posterior border of the mandible; Mandibular height (MH); Inferior diastema length (IDL): from the posterior point of the incisor at its alveolus to the posterior border of the alveolus of M_1; Inferior alveolar length of the lower molars (IAL).

The two character sets were analysed separately. Although in rodents the skull and the mandible form two structures that are highly integrated in their function and during growth, they were analysed independently as they represent sets of genes reflecting different levels of co-adaptation.

Data were transformed into logarithms to render character relationships linear.

The sample includes individuals from both sexes (Tab. 1) and we tested for possible significant effects of sexual dimorphism over the characters by means of two way analysis of variance (unbalanced design), testing for population and sex differences, and for their interaction. A significant interaction of sex with population would suggest that a particular character is sexually dimorphic; therefore, it should be necessary to perform analyses independently for each sex, while no significance would allow the data to be pooled irrespective of sex.

The sample comprises adult animals only, all satisfying 3 conditions: a) M^3 erupted (roughly corresponding to age classes 7 up of PATTON and ROGERS 1983); b) over 200 g; and c) body length over 200 mm. In doubtful cases, the choice was based upon a combination of a and b or a and c.

Since we recorded a certain variation in size within each population representing static allometry (KLINKENBERG and ZIMMERMANN 1992) it seemed essential to correct the data for a proper description of the between group variation. The generally known 'BURNABY' procedure (BURNABY 1966) adjusts original data according to the size vector from the pooled within-group covariance matrix (algorithm suggested by ROHLF and BOOKSTEIN 1987). The pooled within-group covariance matrix was then computed and eigenvectors extracted and examined. The first eigenvector was assumed to represent within-group size and the data were adjusted following BURNABY (1966).

Multivariate analysis of variance and canonical variate analysis (CVA) were used to test the 'BURNABY' adjusted data for differences between centroids and to depict a pattern of population variation.

Mahalanobis distances were used to compute UPGMA and to test for congruencies in patterns between the different character sets.

Differences between groups were also investigated for each character through analysis of variance and GT-2 test among means (SOKAL and ROHLF 1981). For such practical purposes as the rapid and precise identification of specimens in collections we used the ratios of each character to the total length of the skull in order to identify appropriate measurements.

Univariate and multivariate analyses were performed with the SAS system for the PC (ver. 6.08) using the procedures ANOVA, GLM, CANDISC, DISCRIM as variously modified in MARCUS and CORTI (1989). A SAS IML procedure from AFEWORK BEKELE et al. (1993) was used to adjust original data following BURNABY (1966).

Results

Two-way analysis of variance showed a significant effect of sexual dimorphism in only one out of the 19 skull characters, i.e. IFL (two further characters had $p = 0.055$) and in one out of 4 mandible characters (IDL, Tab. 2). These differences were accepted as negligible and all further analyses were performed by pooling all individuals irrespective of sex. On the contrary, all characters except PL revealed significant differences among populations (Tab. 2).

The eigenvectors were extracted from the pooled within-group covariance matrix of the 19 characters of the skull and examined. The coefficients associated with the first normalised eigenvectors all have the same sign (Tab. 3), and so this vector was taken as representing allometry. Raw data were adjusted following BURNABY (1966) and the new data matrix excluding the allometric effect was subjected to canonical variate analysis (CVA).

The first three canonical variates computed on the skull adjusted data express 59.85 % of total variance (24.35 %, 19.1 % and 16.4 %, respectively). To obtain 90 % of variance it is necessary to reach the seventh canonical variate. However, the variance expressed by the 4th to 7th canonical variates decreases from 11.47 % to 3.96 %, and we accepted the scenario depicted by the first three as representative of population variation.

The population ordination onto these first three variates is shown in the stereogram in figure 3. *P. trinitatis* has the highest score on CV1 and the lowest on CV2, *P. canicollis* has

Table 2. **Skull and mandible characters**

Analysis of variance testing for population and sex differences and for the interaction of sex with populations

Character	Obs.	F	p	Character	Obs.	F	p
TL	234	2.77	.0022	UDL	254	4.79	.0001
		17.62	.0001			13.2	.0003
		1.25	.2555			1.32	.214
NL	236	2.66	.0033	IFL	254	4.39	.0001
		15.65	.0001			4.88	.0281
		1.12	.3434			1.9	.0401
CH	250	7.9	.0001	UAL	256	5.49	.0001
		8.42	.0041			.02	.8805
		1.54	.1187			1.8	.0556
BZW	253	3.59	.0001	FMW	254	7.4	.0001
		10.21	.0016			.49	.4843
		.89	.5546			1.03	.4246
MLOW	256	5.85	.0001	PAW	256	2.08	.0228
		18.44	.0001			.34	.5598
		.75	.69			.54	.872
CW	255	3.51	.0001	IFW	253	3.12	.0006
		12.10	.0006			.58	.4475
		.42	.9477			.58	.8445
PL	256	.83	.6062	BTL	255	6.76	.0001
		.07	.7985			3.33	.0692
		.49	.9093			.96	.4869
BL	248	2.03	.0266	ML	256	3.07	.0001
		12.94	.0004			10.00	.0012
		1.11	.356			1.11	.357
IZL	253	2.57	.0044	IDL	256	19.37	.0001
		8.33	.0043			11.25	.0009
		1.65	.0875			2.45	.0007
PLL	254	4.51	.0001	IAL	256	3.31	.0005
		11.36	.0009			0.03	.0622
		1.51	.1273			1.45	.1500
MXHR	254	5.75	.0001	MH	256	2.95	.0017
		7.99	.0051			3.70	.0532
		1.36	.1949			1.07	.0300
BTW	255	7.49	.0001				
		7.85	.0055				
		1.8	.0554				

First row: population; second row: sex; third row: sex-population interaction, with number of observations, F- value and probability. For character abbreviations see text

low score on CV2. CV3contributes in separate *P. poliopus* with the lowest value and the three *Proechimys* sp. (2n = 62) which have the highest. The *P. guairae* populations have intermediate scores on the three canonical variates. The latter are very similar except for *P. guairae* "Oriente", which has a low value onto CV2.

All between group comparisons are highly significant ($p < 0.001$), as is shown by Hotelling's T^2 on Mahalanobis distances (Tab. 4).

The a posteriori probability of correct classification based upon Mahalanobis distances from group centroids lies between 96 % and 72.73 % (average 87.11 %); most of the incorrectly classified individuals fall within other populations of their own species, thus

Table 3. **19 eigenvalues extracted from the pooled within-group covariance matrix of the skull characters, and the character coefficients associated with the first eigenvector**

Eigenvalues 1–19	Character	Eigenvalue 1 coefficients
36.545	TL	0.489
1.1404	NL	0.239
0.6272	BZW	0.167
0.5703	MLOW	0.059
0.4911	CW	0.096
0.3790	BL	0.399
0.3325	IZL	0.335
0.3214	PL	0.060
0.2980	PLL	0.190
0.2499	UDL	0.129
0.2204	IFL	0.081
0.1913	UAL	0.047
0.1897	FMW	0.091
0.1561	PAW	0.051
0.1161	IFW	0.033
0.1018	BTL	0.076
0.0919	BTW	0.035
0.0807	MXHR	0.104
0.0402	CH	0.034

For abbreviation see text.

suggesting that these distances are a good index of between-species differences. These high values of correct classification decrease when group membership is computed using a Jack-knife restriction (crossvalidate option in SAS) to a range lying between 52.38 % and 88 % (average 69.97 %). However, most of the incorrect classifications are still shared within the *P. guairae* complex.

Although Mahalanobis distances are not characterized by a wide range of variability (2.87–6.04) (Tab. 4), they nevertheless reflect species and population distinctions: *P. trinitatis* and *P. canicollis* have, on average, the highest distances, and the lowest are those between populations of the same species (Tab. 4).

The UPGMA phenogram in figure 4 depicts population relationships based on these distances: *P. trinitatis* and *P. canicollis* are very different, the three *Proechimys* sp. (2n = 62) populations are clustered together and connected with the *P. guairae* complex, which forms a homogeneous group. As also shown by the plot in figure 3, *P. guairae* "Oriente" is remarkably distinct form the other *P. guairae* populations, and in the UPGMA it is linked with *P. canicollis.*

CVA was also performed on the log transformed raw data of the mandible. The first two canonical variates account for 94.55 % of total variation (82.47 % and 12.07 %

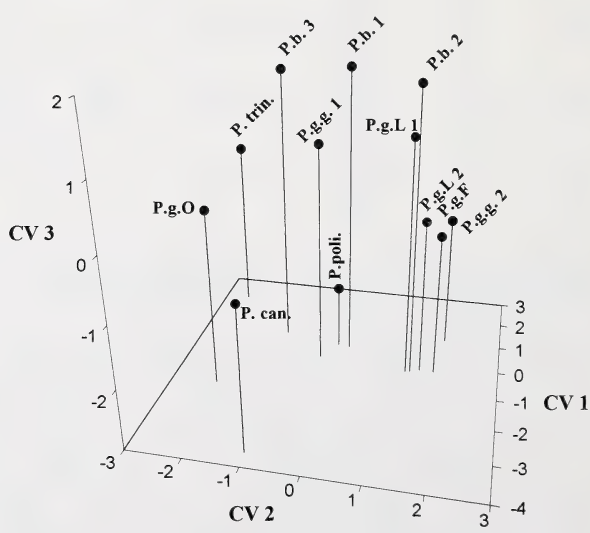

Fig. 3. Stereo scatter plot of population means for the skull onto the first three canonical variates. Units along axes are pooled within-group standard deviations. See Tab. 1 for population acronyms

Table 4. **The matrix of Mahalanobis distances between group centroids for the skull (upper row) and the mandible (lower row)**

Proechimys sp. (2n = 62) (P.b. 1)	—										
	—										
Proechimys sp. (2n = 62) (P.b. 2)	2.87***										
	1.53***										
P. canicollis (P. can)	5.34***	5.20***									
	3.62***	3.69***									
P. guairae "Falcon" (*P.g.* F)	3.56***	3.58***	4.59***								
	1.24**	0.58	3.32***								
Proechimys sp. (2n = 62) (*P.b.* 3)	2.98***	4.07***	5.62***	4.58**							
	1.54***	2.51***	2.44***	2.00**							
P. guairae "Llanos" (*P.g.* L 1)	4.01***	3.78***	5.56***	3.38**	4.35***						
	0.66	1.06	3.31***	0.61	1.56**						
P. guairae "Llanos" (*P.g.* L 2)	4.24***	3.98***	5.51***	2.69**	5.05***	3.25***					
	1.61***	1.71***	2.55***	1.20*	1.41**	1.17*					
P. g. guairae (*P.g.g.* 2)	3.84***	3.75***	5.75***	2.72**	4.80***	4.07***	3.51***				
	1.43***	0.82	3.48***	0.45	2.16***	0.84*	1.14*				
P. g. guairae (*P.g.g.* 1)	3.42***	4.49***	5.15***	3.83**	4.00***	3.49***	3.83***	4.46***			
	0.96*	1.12**	3.15***	0.94*	1.68***	0.76	1.58***	1.37***			
P. guairae "Oriente" (*P.g.* O)	4.08***	4.80***	4.04***	4.91***	4.03***	4.80***	4.88***	5.38***	4.11***		
	4.38***	5.06***	2.03***	4.57***	2.86***	4.31***	3.63*	4.70***	4.27***		
P. poliopus (P. poli)	3.99***	4.37***	5.11***	3.67***	4.16***	4.49***	3.76***	3.56***	4.05***	3.95***	
	1.25***	1.21***	2.64***	0.74	1.40***	0.72	0.91	1.04**	0.77	3.86***	
P. trinitatis	4.52***	5.38***	6.04***	4.92***	4.21***	5.54***	5.59***	5.02***	4.64***	4.69***	4.51***
	0.57	1.01*	3.40***	0.68	1.65***	0.23	1.34**	0.97*	0.62	4.41***	0.81*
	P.b. 1	*P.b.* 2	*P. can.*	*P.g.* F	*P.b.* 3	*P.g.* L 1	*P.g.* L 2	*P.g.g.* 2	*P.g.g.* 1	*P.g.* O	*P. poli*

$p < 0.05$ = *, $p < 0.001$ = **, $p < 0.0001$ = ***, Hotelling T^2.

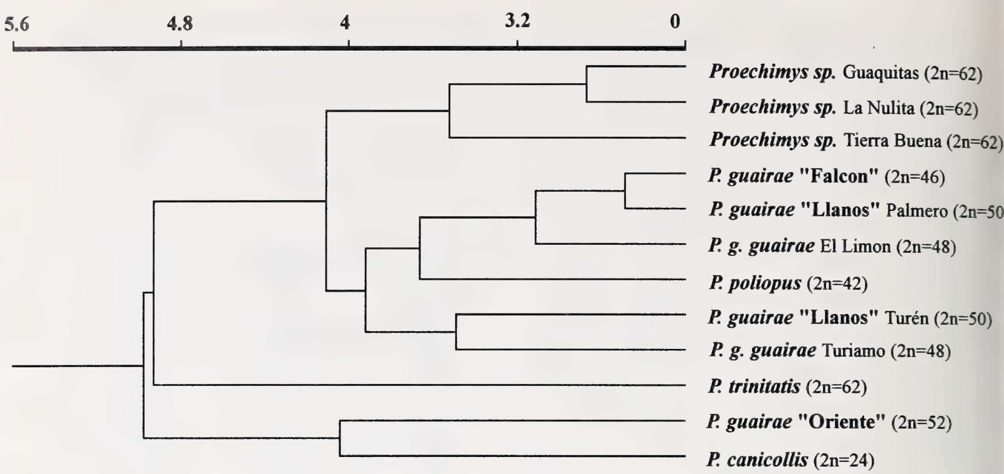

Fig. 4. UPGMA phenogram computed from the Mahalanobis distances between population means for the skull

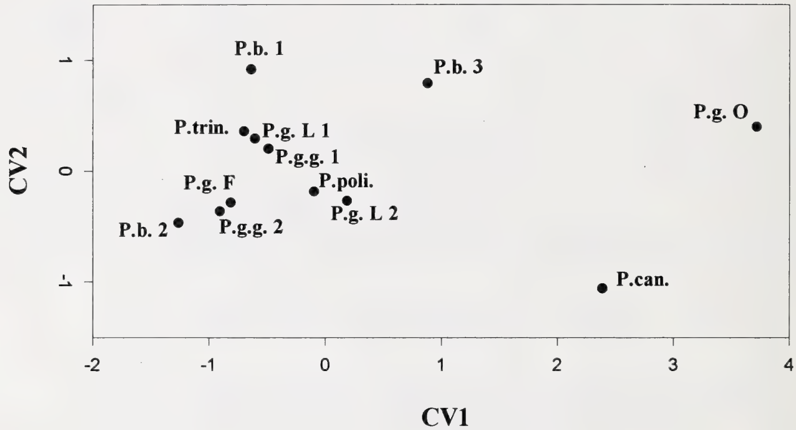

Fig. 5. Scatter plot of population centroids onto first two canonical variates computed on mandible characters. See Tab. 1 for population acronyms

respectively). The scatter plot of population centroids onto first two canonical variates is given in figure 5. CV1 produces a separation of *P. canicollis* and of *P. guairae* "Oriente", which have positive values, from all the others, which have negative values. Lengths of diastema and of alveolar tooth row and mandible height contribute mainly to CV1 and CV2, with pooled within-class standardised character coefficients that are at least 3 times greater than the coefficients of mandible length.

P. guairae "Oriente" and *P. canicollis* have the highest Mahalanobis distances and all are highly significant (Hotelling's T^2, Tab. 4). Distances between the other populations vary without regard to systematic relationships (Tab. 4); for example, Mahalanobis distances between populations of the same subspecies are usually high while distances between populations of different subspecies or species may not be (Tab. 4).

However, a Mantel test between Mahalanobis distances derived from the skull and

those derived from the mandible shows that the two are significantly correlated (r = 0.388, p = 0.0254), i.e. the analyses on the two skeletal components depict a congruent pattern of population differentiation.

We also performed a Mantel test between the skull Mahalanobis distances and the linear geographic distances measured between the collecting sites. The correlation proved to be significant (r = 0.358, p = 0.0164). However, the correlation coefficient increases when the test is performed within the *guairae* complex only (r = 0.40096, p = 0.0064), i.e. when the two allospecies *P. trinitatis* and *P. canicollis* are excluded.

Analysis of variance on character ratios showed that they all differ significantly ($p < 0.01$) except BL, PL, IZL and CW. GT-2 comparisons revealed that significant differences among means are differently scattered, some of the characters exhibiting a homogeneous pattern of differences. There are few significant differences among means within the *P. guairae,* and most of the significant differences are related to the other species. Among these, NL and PAW distinguish *P. poliopus,* UAL, BTL and FMW are unique for *P. trinitatis,* and BTW, IFW and IFL for *P. canicollis.* UDL and CH distinguish *P. canicollis* and *P. guairae* "Oriente" and MXHR *P. guairae* "Llanos", *P. guairae* "Oriente" and *P. trinitatis.*

Discussion

There is no completely positive answer to the first question on the morphometric identification of karyomorphs. Morphometric distinction is clear for those species that have already been recognized and reported in the literature (e.g. Patton 1987; Gardner and Emmons 1984; Reig et al. 1980). Differences in morphometric traits are less evident among the speciating taxa of the *guairae* complex. This is in agreement with the allozyme analysis from Benado et al. (1979) who showed that genetic distances within the rassenkreis are low compared to those with *P. trinitatis* (their *P. urichi;* Aguilera et al 1994).

There is a clear morphometric distinction between *P. canicollis* (the only species forming the *canicollis* group) and the *trinitatus* group. Mahalanobis distances and the UPGMA phenogram clearly highlight this differnce. This is in agreement with Patton's (1987) hypothesis that *P. canicollis* forms a well differentiated group.

Of greatest interest is the *trinitatus* group, in which multivariate morphometrics show a high degree of differentiation among populations. *P. trinitatis* has the highest distinction in skull shape within this group. This species is restricted to a small area in eastern Venezuela and Trinidad island, and morphometric differentiation may be a consequence of a longer time of divergence resulting from the different routes of range expansion of the genus.

Within the superspecies *P. guairae, P. poliopus* (already accepted as a different species by Reig et al 1980) shows a high morphometric differentiation, as well as *P. guairae* "Oriente", which occurs in east Venezuela in a limited area. Moreover, it is interesting to note that the UPGMA based upon skull Mahalanobis distances allows a distinction to be made between the three populations of *Proechimys* sp. (2n = 62) and the other subspecies of the rassenkreis. It has been proposed by Aguilera et al (1994) that the former should be considered as a new species, and their morphometric distinction suggests that the trend in the change of morphology of the skull is congruent with their chromosomal differentiation. All populations of the *P. guairae* (i.e. *P. g. guairae, P. guairae* "Falcon", *P. guairae* "Llanos") share the same sort of morphological modifications and the relationships among them are partially congruent with modifications in karyotype.

Some of the character ratios (the ratio between each character and total length of the skull) are of help in identifying the allospecies, i.e. *P. trinitatis, P. canicollis,* and *P. guairae* "Oriente". It is not possible to perform a-posteriori identification of specimens from the *guairae* complex using any individual character as ratio or as raw measurement, and

morphometric distinction is clear only in a multivariate context, as, for example, for the species *Proechimys* sp. (2n = 62) which is clearly distinct.

There is one question relative to morphometric differentiation in this speciose group: Are the morphological changes reported here a by-product of chromosomal speciation, or do they represent independent adaptation to local ecological conditions?

The fact that there is a significant correlation (although not particularly high) between morphometrics and geography across all populations, and that this correlation is even stronger within the *guairae* rassenkreis, indicates that morphometric differentiation originated in the course of the successive events of speciation coupled with chromosomal change. Therefore, our results are in favour of a phylogenetic cause for the morphometric divergence among population and species.

Reig et al. (1980) hypothesized that speciation in the rassenkreis occurred following the stasipatric model of White (1968). In this context, morphometric differences are believed to have arisen in a clinal model where primary integration zones progressively evolved to form tension zones across which gene flow is highly limited if not absent. However, the following alternative model of chromosomal speciation adopted by Reig (1980) and subsequently accepted by Aguilera et al. (1994) favours the hypothesis of speciation via centric fission as essentially peripatric (Mayr 1982), following an increase in diploid number. "This process was repeated several times under the influence of cycles of forest retraction and expansion determined by the Pleistocene climatic fluctuations" (Reig et al. 1980, p. 308). If this is true, morphological differentiation in the superspecies *Proechimys guairae* is a direct product of speciation of small peripheral isolates occurring over the last 50,000 years (Benado et al. 1979).

Acknowledgements

This study has been supported by CONICIT, grant S1-1274 (O. A. Reig and M. Aguilera), by Decanado Investigacines-USB (M. Aguilera), by CNR, Progetto bilaterale "Composizione genomica e speciazione cromosomica nei roditori" no. 93.00233.CT04 (M. Corti), and by MURST, Fondi di Ateneo Università di Roma 'La Sapienza', quota 60 % "Meccanismi di speciazione in ambiente tropicale" (M. Corti).

Zusammenfassung

Kraniometrische Differenzierung und chromosomale Artbildung in der Gattung Proechimys (Rodentia: Echimyidae)

Mittels multivariater morphometrischer Methoden wurden die Systematik und die geographische Variation der Gattung *Proechimys* in Venezuela untersucht. Die erfaßten Populationen zeigen ausgeprägte Unterschiede hinsichtlich des jeweils vorkommenden Karyotyps (2n = 24 – 2n = 62). Die auf Schädel- und Mandibelmerkmalen beruhende morphometrische Differenzierung in der Gattung *Proechimys* unterstützt die Hypothese, daß aufeinanderfolgende Artbildungsereignisse mit einem Anstieg der diploiden Chromosomenzahl einhergingen. Während sich die jeweiligen Einzelmerkmale diesbezüglich als unzureichend erwiesen, waren alle Arten und Unterarten mit multivariaten Verfahren klar unterscheidbar.

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Authors' addresses: Marisol Aguilera, Departamento Estudios Ambientales, Universidad Simon Bolivar, Apdo. 89.000, Caracas, YV-1081-A, Venezuela, and Marco Corti, Dipartimento di Biologia Animale e dell'Uomo, Università di Roma 'La Sapienza', Via Borelli 50, I-00161 Roma, Italy

Z. Säugetierkunde 59 (1994) 378–379
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ISSN 0044-3468

WISSENSCHAFTLICHE KURZMITTEILUNGEN

Cases of dental malocclusion in populations of Red foxes (*Vulpes vulpes*) in the state of Victoria, Australia

By E. Meijaard and P. J. H. van Bree

Department of Mammalogy, Zoological Museum, University of Amsterdam, The Netherlands

Receipt of Ms. 28. 1. 1994
Acceptance of Ms. 27. 7. 1994

Bouwmeester et al. (1989) described the high incidence of a pronounced protrusion of the maxillary incisors over the mandibular incisors which they found in skulls of red foxes (*Vulpes vulpes*) in the North Holland Dune Reserve (NDH) in the Netherlands. This aberration was present in 6.7 % of the skulls and proved, through skull measurements, to be the result of a shortening of the front part of the mandibles. The aberration was thought to be under monogenetic control. Its high incidence could be explained by the history of the fox population in the NDH. Before 1968 the NDH was not inhabited by red foxes. In that year four cubs from the same litter were set free, thus creating a small and isolated gene pool. Compared to normal red foxes, affected animals are likely to be at an ecological disadvantage. Bouwmeester et al. (1989) expect the incidence of the aberration to decline in the future. This view is supported by the fact that among several thousand red foxes from England, where no such genetic bottleneck occurred, such anomaly was found only a couple of times. Not one case was reported among several thousand red foxes from Sweden (Bouwmeester et al. 1989).

In a study on skulls of red foxes from Australia three out of 39 skulls (= 7.7 %) showed

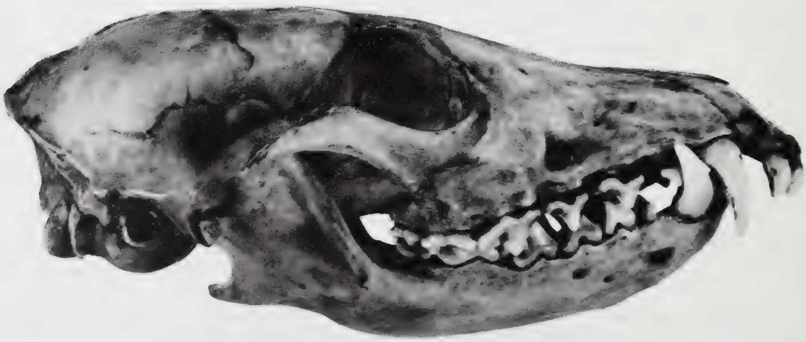

Fig. Skull of female fox, *Vulpes vulpes*, from around Geelong, Victoria, Australia, I-1989 (ZMA 24.065) with shortened mandibles

a similar shortening of the mandible. These skulls were collected around Geelong, Victoria (38° 27′ S, 144° 51′ E). In a collection of 22 skulls from the Western Australian Museum in Perth one skull (= 4.5 %) showed the aberration. Palatal length was not measured on this specimen. All the 56 fox skulls in the collection of B. J. COMAN (at Strathfieldsaye, Australia) which were mostly from different areas in Victoria, were normal, just like 42 skulls from the Museum of Victoria in Melbourne and 5 skulls from the Australian Museum in Sydney.

Considering the history of Australian red foxes, which were introduced in Australia over 130 years ago (ROLLS 1969) and have been isolated since then, the incidence of the aberration was thought to be remarkably high, i.e. 2.5 % of all the skulls mentioned above.

The Figure shows a specimen with shortened mandible out of the Geelong area.

To investigate the character of this aberration a number of skull measurements were taken, namely condylo-basal length, palatal length and mandible length. By calculating the palate/condylo-basal ratio and the mandible/condylo-basal ratio and by comparing these calculations with the values for normal red foxes from the sample, it became clear that this was a case of shortened mandibles. This is important to know because the aberration could also have been caused by an elongated rostrum (BOUWMEESTER et al. 1989).

It goes beyond the scope of this contribution to speculate on causes of the established high incidence of the aberration. Further research is needed on genetic and ecological backgrounds to elucidate the reason for the described phenomenon. It seems, however, that the small founder population in Australia has played an important role.

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Authors' address: E. MEIJAARD and Dr. P. J. H. VAN BREE, Institute for Systematics and Population Biology (Zoological Museum), Mauritskade 61, NL-1092 AD Amsterdam, The Netherlands

Z. Säugetierkunde 59 (1994) 380–381

ISSN 0044-3468

Eliomys (*Hypnomys*) *onicensis* nomen novum, to replace the homonym *Hypnomys intermedius* Reumer, 1981 (Rodentia: Gliridae) from Majorca

By J. W. F. Reumer

Natuurmuseum Rotterdam, Rotterdam, Niederlande

Receipt of Ms. 15. 3. 1994
Acceptance of Ms. 20. 7. 1994

In 1981, I described the endemic dormouse *Hypnomys intermedius* from the Pleistocene of Majorca (Reumer 1981). The name was chosen for the intermediary position the species takes in the evolutionary lineage leading from *H. waldreni* Reumer, 1979 to *H. morpheus* Bate, 1944. The position of the Mediterranean island glirids within the tribal framework of the family was at that time unknown (Daams 1981). Some thirty years earlier, Friant (1953) had described a subspecies of dormouse from the Ruscinian of Sète (southern France), which is now known as the species *Eliomys intermedius* Friant, 1953.

Zammit Maempel and de Bruijn (1982) were the first to include the endemic Mediterranean glirid genera as subgenera within *Eliomys* Wagner, 1840. This opinion is since followed, e.g. by Moya-Sola et al. (1984) and by Alcover and Agusti (1985).

Hypnomys intermedius Reumer, 1981 was considered by Zammit Maempel and de Bruijn (1982) to be a junior synonym of *H. eliomyoides* Agusti, 1980 from the Balearic island of Menorca. However, Agusti and Moya-Sola (1990) considered *H. intermedius* and *H. eliomyoides* to be two valid species, based on morphological differences.

These opinions leave us with *Eliomys (Hypnomys) intermedius* Reumer, 1981 as a valid species. It is then a homonym of *Eliomys intermedius* Friant, 1953. A nomen novum is therefore necessary, for which I propose

Eliomys (*Hypnomys*) *onicensis* nomen novum

The name is derived from the type locality (Sa Pedrera de S'Onix, Porto Cristo, Majorca).

It is noteworthy in this context that Agusti (1986) writes: "*Hypnomys* is considered to evolve from *Eliomys intermedius* Friant."

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Authors' address: Dr. Jelle W. F. Reumer, Natuurmuseum Rotterdam, P. O. Box 23452, NL-3001 KL Rotterdam, The Netherlands

Protokoll über die außerordentliche Mitgliederversammlung der Deutschen Gesellschaft für Säugetierkunde e.V. am 16. Juli 1994 im Großen Hörsaal des Zoologischen Instituts der Universität Bonn

Der 1. Vorsitzende, Herr SCHMIDT, eröffnet die Versammlung um 13.00 Uhr.

1. Die Tagesordnung wird angenommen.
2. Zeitschrift für Säugetierkunde:
   Herr SCHMIDT schildert die Chronologie der Aktivitäten der Gesellschaft seit dem unrechtmäßigen Verkauf der Verlagsrechte durch den Parey-Verlag an den Verlag Blackwell-Wissenschaft, Berlin. Er gibt bekannt, daß sechs Verlage daran interessiert sind, die Herausgabe der traditionsreichen „Zeitschrift für Säugetierkunde" ab Band 60 (1995) zu übernehmen. Es sind dies Aula/Wiesbaden, Birkhäuser/Basel, Blackwell/Berlin, Ferdinand Enke/Stuttgart, Gustav Fischer/Jena, Walter de Gruyter & Co./Berlin. Herr SCHMIDT schildert kurz die Vorzüge und Nachteile des jeweiligen Angebotes und gibt bekannt, daß der Vorstand unter Abwägung aller Gesichtspunkte (z. B. Renommee des Unternehmens, Verlagsprogramm, Zuverlässigkeit in der Herstellung, Kooperation mit der Schriftleitung, Preisgestaltung, Format) sich dazu entschlossen hat, der außerordentlichen Mitgliederversammlung vorzuschlagen, der Reihenfolge nach mit folgenden Verlagen Kontakt aufzunehmen: Fischer, Birkhäuser, de Gruyter, Enke.
   In der anschließenden Diskussion wird die Frage, ob es sinnvoll sei, die Zeitschrift in Eigenregie herauszugeben, erörtert und abschlägig beschieden. Eine weitere Frage gilt der wirtschaftlichen Situation des Verlags Fischer, Jena; sie wird vom Vorstand als gesund bezeichnet. Geheim und schriftlich stimmen danach die Anwesenden über den Vorschlag des Vorstandes ab, bei Parey zu kündigen und Verhandlungen mit anderen Verlagen in der vorgeschlagenen Reihenfolge aufzunehmen. Das Ergebnis: 23 Ja-Stimmen, keine Gegenstimme und keine Enthaltung.
3. Verschiedenes:
   Hierzu wird die Frage erörtert, ob es sinnvoll sei, eine automatische Abbuchung der Mitgliederbeiträge vorzunehmen. Die Mehrheit spricht sich aus Kostengründen dagegen aus.
   Um 14.00 Uhr schließt der 1. Vorsitzende die Versammlung.

Prof. Dr. U. SCHMIDT 1. Vorsitzender	Prof. Dr. H. ERKERT Geschäftsführer	Dr. H. FRÄDRICH Schriftführer

Protokoll über die Mitgliederversammlung der Deutschen Gesellschaft für Säugetierkunde e. V. am 26. September 1994 im Hörsaal des Biozentrums der Universität Wien

Der 1. Vorsitzende, Herr SCHMIDT, eröffnet die Versammlung um 16.30 Uhr und gibt unter dem Beifall des Auditoriums bekannt, daß Herr TEMBROCK, Berlin, zum Ehrenmitglied ernannt wurde.

1. Die Tagesordnung wird angenommen.
2. Der Geschäftsführer, Herr ERKERT, verliest den Bericht über das Jahr 1993. Die 67. Hauptversammlung der Gesellschaft fand auf Einladung von Herrn MAIER vom 26. September bis 1. Oktober 1993 in Tübingen statt; sie tagte dort gemeinsam mit der Gesellschaft für Primatologie. Ein zusätzlicher Tag galt Fragen des Fledermausschutzes. Schwerpunktthemen waren „Offene Fragen der Phylogenie und Systematik der

Großgruppen", „Geruchssinn und olfaktorische Kommunikation" sowie „Biologie der Primaten". Mit 75 Vorträgen und 45 Postern war die Veranstaltung ein Erfolg. Der Fritz-Frank-Förderpreis der DGS wurde an Herrn Dr. Thomas Martin, Berlin, für seine Arbeit „Schmelzmikrostruktur in den Inzisiven alt- und neuweltlicher hystricognather Nagetiere" vergeben. Drei Poster wurden mit Buchpreisen bedacht, die der Parey Verlag dankenswerterweise gestiftet hat. Herr Erkert dankt den Veranstaltern, Herrn Maier und Herrn Fischer, für die Ausrichtung, Herrn Niemitz und Herrn Müller für die organisatorische Unterstützung der erfolgreichen Tagung.
Im Berichtsjahr erschien der 58. Band der „Zeitschrift für Säugetierkunde" in sechs Heften mit insgesamt 384 Seiten; den beiden Schriftleitern und den aktiven Herausgebern wird gedankt. Die Mitgliederzahl hatte sich bis Ende 1993 auf 622 geringfügig erhöht. Durch den Tod verlor die Gesellschaft folgende Mitglieder:

Prof. Dr. Fritz Strauss, Wabern/Schweiz
Prof. Dr. Martin Eisentraut, Bonn
Herr Hubert Merz, Langenbach.

3. Die Satzungsänderungen sind durch Eintragung in das Vereinsregister des Amtsgerichtes Berlin-Charlottenburg nunmehr wirksam geworden. Die neue Satzung und das Mitgliederverzeichnis gehen den Mitgliedern mit der nächsten Aussendung zu.
4. Herr Erkert erläutert den von Frau Kühnrich abgefaßten detaillierten Kassenbericht und dankt Frau Kühnrich für ihre sorgfältige und effektive Arbeit.
5. Die Herren Bohlken und Schliemann haben die Konto-Unterlagen der Gesellschaft in Hamburg geprüft und für korrekt befunden.
6. Die Anträge auf Entlastung der Schatzmeisterin und des Vorstandes werden bei Enthaltung des Vorstandes angenommen.
7. Die Herren Bohlken und Schliemann werden bei einer Enthaltung als Kassenprüfer für das Geschäftsjahr 1994 gewählt. Beide sind mit der Wahl einverstanden.
8. Der Vorstand schlägt vor, die Mitgliedsbeiträge für 1995 unverändert zu lassen. Dies wird bei einer Enthaltung angenommen.
9. Die Mitgliederversammlung nimmt die Einladung von Herrn Fischer an, die 69. Jahrestagung vom 24. bis 28. September 1995 in Göttingen abzuhalten. Als Schwerpunktthemen sind vorgesehen „Säugetiere in der Kulturlandschaft", „Fortpflanzungsbiologie", „Chronobiologie/Aktivitätsrhythmen".
   Per Akklamation wird die Einladung von Herrn Kruska angenommen, der für das Jahr 1996 nach Kiel eingeladen hat.
10. Herr Schmidt berichtet, daß wegen der kritischen Situation der „Zeitschrift für Säugetierkunde" am 16. Juli 1994 eine außerordentliche Mitgliederversammlung in Bonn stattfinden mußte, die leider nur schlecht besucht war. Herr Erkert trägt den gegenwärtigen Stand der Verhandlungen mit dem Parey Verlag vor und berichtet, daß Kontakte mit dem Fischer Verlag, Jena, als möglichem künftigen Herausgeber aufgenommen wurden. Obgleich es derzeit noch ungeklärte juristische Fragen gibt, wird der Vorstand alles versuchen, das Erscheinen des Bandes 60 zum frühestmöglichen Zeitpunkt zu bewirken.
11. Die Kommissionen und Arbeitsgruppen der DSG berichten über ihre Tätigkeit.
    a) Erneut wird kritisiert, daß von der Tierschutz-Kommission noch immer kein ausführlicher Bericht vorliegt. Bei der anschließenden Diskussion wird deutlich, daß die Arbeit gerade dieser Kommission zugegebenermaßen schwierig ist. Dennoch drängen die Diskussionsteilnehmer darauf, daß die Tierschutzkommissions-Mitglieder ihre Arbeit beschleunigen.
    b) Herr Schröpfer berichtet über aktuelle Probleme im Hinblick auf Tier- und Artenschutzämter und wird von der Versammlung beauftragt, eine Artenschutz-Kommission zu gründen, welche die Zielsetzungen und Forderungen der DGS definieren soll.

c) Herr HEIDECKE trägt die Aktivitäten der Biber- und Bisamgruppe vor.
d) Herr FRÄDRICH berichtet über das erste Treffen der Arbeitsgemeinschaft Tiergartenbiologie, das Ende 1993 in Erlangen erfolgreich abgehalten wurde. Er gibt bekannt, daß die zweite Tagung dieser Art auf Einladung von Herrn GANSLOSSER vom 11. bis 13. November 1994 ebenfalls in Erlangen stattfinden soll.
e) Herr SCHMIDT berichtet über die Aktivitäten der „Koordinationsgruppe Fledermausschutz" sowie über die erfolgreiche Tagung, die vom 22. bis 25. Juli 1994 in Bonn stattgefunden hat.
f) Die Versammlung begrüßt den Antrag von Herrn UHR, eine Arbeitsgemeinschaft über das Thema Domestikation ins Leben zu rufen, und beauftragt ihn, dazu geeignete Schritte zu unternehmen.

12. Herr SCHMIDT bittet die Anwesenden um Unterzeichnung eines Glückwunschbriefes an Herrn HERRE, der im Mai 1994 85 Jahre alt wurde.
Der von Herrn HUTTERER formulierte Glückwunschbrief zum 75jährigen Jubiläum der amerikanischen Säugetiergesellschaft ist dort mit Genugtuung aufgenommen worden. Die amerikanischen Kollegen schlugen vor, zu gegebener Zeit beide Gesellschaften gemeinsam tagen zu lassen.

Die Sitzung endet um 18.35 Uhr.

Prof. Dr. U. SCHMIDT	Prof. Dr. H. ERKERT	Dr. H. FRÄDRICH
1. Vorsitzender	Geschäftsführer	Schriftführer

10th International Bat Research Conference 25th North American Symposium on Bat Research

The 10th International Bat Research Conference and 25th North American Bat Research Conference will be held at Boston University, Boston, Massachusetts, USA (7–12 August 1995). This joint conference will include: Plenary addresses, symposia, contributed papers, poster papers, films/videos, workshops, and excursions. Questions concerning this conference should be addressed to: 10th International Bat Research Conference, Department of Biology, Boston University, Boston, Massachusetts 02215, USA.

Erscheinungsweise und Bezugspreis 1994: 6 Hefte bilden einen Band. Jahresabonnement Inland: DM 378,– zuzüglich DM 13,80 Versandkosten; Jahresabonnement Österreich: öS 2949,– zuzüglich öS 164,– Versandkosten; Jahresabonnement Schweiz: sfr 364,– zuzüglich sfr 21,– Versandkosten; Jahresabonnement EG-Binnenmarkt-Länder mit USt-ID-Nr.: DM 353,27 zuzüglich DM 19,63 Versandkosten; Jahresabonnement EG-Binnenmarkt-Länder ohne USt-ID-Nr. und Drittländer: DM 378,– zuzüglich DM 21,– Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey GmbH & Co. KG, Spitalerstraße 12, D-20095 Hamburg, Bundesrepublik Deutschland, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde“ erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Z. Säugetierkunde 59 (1994) 6, 321–384

Mit dem Bandinhaltsverzeichnis